

**Maximizing peatland forest regeneration success at lowest  
cost to the atmosphere: Effects of soil preparation on  
Scots pine seedling vitality and GHG emissions**

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Academic dissertation

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This dissertation investigated the impacts of soil preparation after clearcutting Scots pine (*Pinus sylvestris* L.) forest on thick-peated soil from silvicultural and climatic standpoints. Three growing seasons after outplanting, mounding most effectively secured seedling survival, growth, and vitality through improved soil aeration of the planting spot. However, other presumed benefits of mounding to seedlings such as warmer soil temperatures and faster organic matter decomposition were not confirmed here. Regeneration in scalps was unsuccessful due to waterlogged soil. Importantly when scalping, only the humus layer should be scraped off without creating depressions in the peat. Seedling tolerance to desiccated as well as waterlogged peat soil over one growing season was remarkable in controlled conditions. The impact of drought, however, was more immediate and severe as root and shoot growth, fractional colonization of ectomycorrhizal fungi, and root hydraulic conductance were reduced. Nevertheless, maintenance of rather high photochemical efficiency (expressed as variable to maximal chlorophyll fluorescence,  $F_v/F_m$ ) especially in current-year needles despite harsh drought seemed to indicate a potential for seedling recovery. Polyamine analysis also revealed that new needles are preferred in protecting the different parts of the seedlings against drought stress. Wet-stressed seedlings, on the other hand, exhibited few signs of suffering. It was also demonstrated how the experimental environment—a controlled versus field setting—influences seedling tolerance to stress. The differing moisture levels within comparable microsites—dry vs. wet scalps and ditch vs. inverted mounds—had little influence on seedling growth and condition although physiological upset (i.e.,  $F_v/F_m$ ) was evident within scalps. Namely, the wetter the soil was, the lower  $F_v/F_m$  was.

The fear of soil preparation accelerating GHG emissions, particularly CO<sub>2</sub>, from peat into the atmosphere appears unwarranted at least on nutrient-poor, boreal forestry-drained peatland sites. The overall climatic impact of soil preparation, in the forms of mounding and scalping, three years after application expressed in terms of CO<sub>2</sub> equivalents (100-year GWP), was neutral compared to leaving soil unprepared.

The core findings of this research support mounding as the best alternative on nutrient-poor, drained peatland sites when the goal is to maximize the regeneration success of Scots pine after clearcutting with minimal impact on soil GHG emissions. In the future, development of soil preparation methodology is particularly deserving of further attention. While it may not be the sexiest research topic in the worldwide rat race of the modern day, it is nonetheless of substantial importance in a country highly specialized not only in the utilization but also the rejuvenation of wood resources on drained peatlands.

**Keywords:** forestry-drained peat soil, clearcutting, mounding, scalping, CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O fluxes, drought and waterlogging stress

## PREFACE

One-sixth of my life has elapsed while making this discourse set before you. Six years later, I do admittedly wonder what in the almighty universe ever possessed me to embark on the Journey to the Ultimate Abyss. I faintly recall swearing over administrative tasks one preposterous day and romanticizing of field work related to my study discipline, peatland forestry, complete with blood, sweat, and tears and pin-up ditch-digging, topless hunks. My decision was expedited by unexpected news of deteriorating health with an unknown prognosis. It's now or never, as Elvis so fittingly sang. These factors eventually led me to a town of endless enchantment along highway 3, Parkano FI. I soon found myself acting in a scientific soap opera, measuring the invisible, i.e., greenhouse gases, inadvertently getting high on acetone in the garage while maintaining my measuring equipment, speaking in tongues to pine seedlings and praying for them to spare me the anguish and die faster, and wading in a deep, peaty ditch with snowshoes on and my sled upturned and hollering for divine intervention to all wildlife present. As in life in general, the ups and downs escorted me through the PhD project. At times, I was accelerating on an open highway, not a detour in sight, but suddenly road construction bogged me down and forced me to take the scenic route to get to my destination. When road rage hit, I even lost sight of my destination entirely, often being blinded by the headlights of foreboding circumstances and certain only of a future as academic roadkill. But, once the floodgates of anxiety, terror, and all other internal commotion were opened, I was ready to rock and roll again. Indeed, some days I was convinced that the whole world was deviously plotting against me and there was no escaping the predicament, but the very next day my carcass was resuscitated as my primitive call of the wild was mysteriously answered. The battle to collect coherent data on occasion took on surreal proportions. In a migraine delirium, I recollect measuring in the midst of a summertime downpour, umbrella in one hand, chamber in the other while huddling over my analyzer device and shutting my eyes ever so often to ease the urge to puke and faint with strictly one thought reiterating in the warped cerebral context of my mind: guard the device with your life, keep it dry at all times. Such out-of-body experiences are perhaps not recommended in faculty guidelines, but they are apparently part of the process to realize and understand what it means to be human and the limitations it imposes—or should impose. Though scientific research strives for objectivity and truths, I have discovered that as a researcher I am nonetheless inevitably bound by my personal spectrum of emotions, be it passion or madness. Hence, the exhilaration, as if thrust into Shangri-la, upon getting published or receiving funding; or alternatively, the distraught aroused by malfunctioning equipment or the recurrent, cognitive whiplash induced by every disturbing referee comment. Indeed, there's nothing like joy or rage to get my blood flowing.

Along this long and winding road, I am indebted to a number of people who steered me in the right direction professionally and/or personally. Because of them, I have found my limits and identified the healthy boundaries of self-criticism, learned to move forward and cling to hope despite oncoming tornados, and realized that there is no shame in asking for or receiving help.

My sincerest gratitude goes out to Prof. Jukka Laine, Dr. Kari Minkkinen, Markku Saarinen, and Dr. Niko Silvan for their supervision. Jukka, at times I was a nonbeliever, but thanks for always getting my train back on its tracks. Fortunately for me, you are a peacekeeper at heart and an effective sedative for my fiery disposition. Kari, you rose to the occasion and are deserving of my utmost appreciation for coming through when it counted the most. Markku, you kept me above water in my darkest hours and shared the load, you patiently listened, and your expertise and ability to teach are world class. Niko, you speak and instruct in terms I can understand, you supported me when my cup became too full, and you have been a godsend to me in so many ways.

I also wish to thank all the co-authors of the articles. In particular, Dr. Tytti Sarjala for all your enthusiasm and empathy in addition to your remarkable professional talents, and Laura Nummelin for being my official lifesaver the last summer of measurements.

Thanks to my colleagues Dr. Jyrki Jauhiainen and Prof. Raija Laiho for the constructive meetings, which provided necessary inspiration and encouragement from beyond the walls of the project. Raija, I also wish to express my warmest thanks for commenting on my summary and for coaching me in the critical moments of its preparation. To Prof. Harri Vasander, for always looking on the bright side, being helpful and flexible, and humoring me in addition to ensuring the smooth procession of matters related to my studies and this thesis. Many thanks to Prof. Juhani Päivänen for never disappointing and for your undying encouragement and praise over the years. I also want to thank Paavo Ojanen for being an easily approachable genius and technical wizard.

I am also grateful to the pre-examiners Prof. Björn Hånell and Prof. Eeva-Stiina Tuittila for your willingness to immerse yourselves in my dissertation and for the invigorating, positive feedback. Sincere thanks to Dr. Florence Renou-Wilson for agreeing to serve as my opponent. Furthermore, without the financial support provided by the Finnish Cultural Foundation, Research Foundation of the University of Helsinki, Maj and Tor Nessling Foundation, GSForest – Graduate School in Forest Sciences, Niemi Foundation, UH Faculty of Agriculture and Forestry and Dept. of Forest Sciences, this project would only be a figment of my imagination. Your assistance was greatly appreciated.

Finally, I desire to wholeheartedly thank my friends, family, and relatives on two continents for their support, in sickness and in health, during the years although I admittedly am mediocre at keeping in touch. To all those who made a difference but it is not possible to mention by name, I acknowledge you. And to all of those who spoke a few kind words or cracked a crazy joke rooted in empathy during this Journey, I salute you. The little things can, indeed, make the difference between a good day and a catastrophic one. I especially wish to recognize my dear friend Mirkka Kotiaho for giving me the strength to hang on when it least felt like anything could ever come of this Journey. Without the “crisis hotline” and our marathon conversations to vent my stress and frustrations and foam at the mouth, where would I be? Additionally, I would like to thank Anja Laine for your motherly goodwill and all those tasty suppers, and Kaisa Silvan for making me feel welcome from the start and for your rational thinking. Special thanks to my good-hearted parents Paula and Gary Pearson for invariably believing in me. And mom, your ass-kicking attitude, fighting spirit, and cast-iron spine have always been a constant source of inspiration to me. I would also like to thank my uncle, a jack of all trades, for providing practical know-how and on occasion relief with manly tasks in the field. Lastly, I cannot go without honoring the loved ones I have lost during this Journey. To Geoffrey, Don, Peppi, Nan, and Clint, moving on is the hardest thing I know, but the memories make life livable and the impossible attainable.

To all those struggling with a freaking PhD or consumed by the woes of intermittent funding etc., etc., one fine piece of advice: be humane to thyself in addition to those around you, and above all, have faith. In writing this, it feels unreal that the “initiation” is actually coming to a close. Honestly, am I hallucinating?

With peace of mind and high hopes of funding for all,

Meeri Pearson      April 29<sup>th</sup> 2013      Kulju village, Lempäälä

## LIST OF ORIGINAL ARTICLES

This dissertation is based on the following articles, which are referred to by their Roman numerals in the text. In addition, previously unpublished field results related to Study III are presented in the summary.

**I** Pearson, M., Saarinen, M., Minkkinen, K., Silvan, N. & Laine, J. 2011. Mounding and scalping prior to reforestation of hydrologically sensitive deep-peated sites: factors behind Scots pine regeneration success. *Silva Fennica* 45(4): 647–667.  
<http://www.metla.fi/silvafennica/full/sf45/sf454647.pdf>

**II** Pearson, M., Saarinen, M., Heiskanen, J., Sarjala, T. & Laine, J. 2013. High and dry: Consequences of drought exposure in Scots pine seedlings grown in authentic peat soil. *Suo-Mires and Peat* 64(1): 1–22.

**III** Pearson, M., Saarinen, M., Nummelin, L., Heiskanen, J., Roitto, M., Sarjala, T. & Laine, J. Tolerance of peat-grown Scots pine seedlings to waterlogging and drought: The lesser of two evils? (*Submitted manuscript*).

**IV** Pearson, M., Saarinen, M., Minkkinen, K., Silvan, N. & Laine, J. 2012. Short-term impacts of soil preparation on greenhouse gas fluxes: A case study in nutrient-poor, clearcut peatland forest. *Forest Ecology and Management* 283: 10–26.  
<http://dx.doi.org/10.1016/j.foreco.2012.07.011>

M. Pearson is fully responsible for the summary of this doctoral thesis including the previously unpublished field results presented in it. Regarding Studies **I** and **IV**, she was responsible for all the planning, implementation, collection of field data, data analysis and interpretation, and model constructions. In Studies **II** and **III**, she was responsible for most of the planning, implementation, and data collection with the exception of the water retention curve and root hydraulic conductivity measurements at the end of the experiment. She performed the majority of the data analysis and interpretation excluding polyamines and the technical application of the statistical method. In Studies **I–IV**, M. Pearson was the main writer and reviser of the manuscript.

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# 1. INTRODUCTION

## 1.1. Boreal peatlands and forestry

The accumulation of organic matter as peat occurs in regions of the world where precipitation exceeds evapotranspiration. Consequently, the cool, humid climate of the boreal zone provides a hospitable backdrop for peat formation. Due to surplus water and poor oxygen availability, degradation of organic matter is slower than the input rate hence accumulating as peat on the soil surface. At the same time, such soil conditions restrict tree growth. An intact, wet ecosystem that actively accumulates peat is termed a *mire*, whereas an area simply covered by peat, accumulating or not, is deemed a *peatland* (Päivänen and Hånell 2012). Loss of the accumulative function of a peat soil site typically results from anthropogenic interference, for example, drainage.

In Finland, mires and peatlands constitute approximately 29% (9 million ha) of the entire land area (10<sup>th</sup> National Forest Inventory). In order to improve their wood production capacity, mires in Finland have been extensively drained, totaling nearly 5.5 million ha (Päivänen and Hånell 2012). Scots pine (*Pinus sylvestris* L.) predominates on 3.4 million ha of these forestry-drained peatlands (Hökkä et al. 2002). At present, an estimated 390 000 ha of Finnish peatland forests are due for regeneration, and an additional 347 000 ha within the next five years (Saarinen 2011). Pine-dominated stands are at the center of this forthcoming peatland forest renewal. Undoubtedly, the time for enacting functional regeneration strategies, which recognize the unique nature of peat soils, has never been better.

## 1.2. Stand regeneration and soil preparation on forestry-drained peatlands

Forest regeneration success can be defined as the establishment of a new generation of trees of the desired species, which are adequately spaced, sufficient in number, and in robust health with the capacity for continued development to attain the goals of timber production. Peat soil poses several challenges to successful forest regeneration, the foremost of which being to ensure sufficient soil aeration for tree root growth by expelling surplus water from the regeneration site (Mannerkoski 1985). Harvesting of the transpiring tree stand typically causes the water table level (WTL) to markedly rise (Heikurainen and Päivänen 1970, Roy et al. 1997) while also increasing throughfall (of precipitation), snow cover depth, and runoff (Heikurainen and Päivänen 1970, Paavilainen and Päivänen 1995). This phenomenon is often referred to as watering up (e.g., Roy et al. 1997, Marcotte et al. 2008). Wetter circumstances may alter the composition of ground and field layer vegetation and favor regression towards natural mire species (Laine et al. 1995, Hotanen 2003). For instance, cottongrass (*Eriophorum vaginatum* L.) has been shown to spread aggressively after timber harvesting on nutrient-poor drained peatland sites consequently deterring natural regeneration of Scots pine (Kuusipalo and Vuorinen 1981). Other potential obstacles to successful peatland forest regeneration include a thick raw humus layer which inhibits conifer seed germination especially in old drainage areas (Kaunisto 1984), abundant suckering and emergence of natural seed-borne pubescent birch (*Betula pubescens* Ehrh.) seedlings (Saarinen 2002), variability of weather conditions and impact on peat as growing substrate (Saarinen 2005), potassium (K) and/or phosphorus (P) deficiency on thick-peated sites (e.g., Kaunisto 1997), frost heaving, poor bearing capacity of the soil and risk of damage to seed tree root systems (Päivänen and Hånell 2012).

To rectify the WTL rise after stand removal, ditch maintenance (ditch cleaning + supplementary ditching) and soil preparation, often in combination, are measures commonly implemented prior to reforestation. Mounding is the most widely applied method of mechanical soil preparation in drained peatland forest regeneration schemes (Saarinen 1997). It involves the creation of bare peat heaps atop the peatland surface. These mounds serve as havens for establishment of artificially or naturally regenerated conifer seedlings amidst an otherwise challenging environment. Seedlings benefit from the elevated microsite position (Lähde et al. 1981), which for the most part eliminates the problem of waterlogged soil and associated poor aeration although soil moisture will depend somewhat on mound height, peat type, and the mounding technique used (Saarinen et al. 2009). Planting on discontinuous, raised soil heaps has also been found to provoke symmetrical rooting thereby reducing lean and windthrow (Savill 1976). Other assumed advantages of mounding versus leaving soil undisturbed include delaying the spread of competing vegetation, reduced damage to seedlings caused by crawling insects, and warmer soil temperatures in the rooting zone. Warmer and better aerated soil purportedly enhances nutrient mineralization and availability to seedlings by stimulating the organic matter (OM) decomposition process spurred by microbes (Örlander et al. 1990, Sutton 1993, Londo and Mroz 2001). On peatlands, however, the effects of harvesting and soil preparation on OM decomposition and quality are not well known (Prescott et al. 2000, Mäkiranta et al. 2012), and the majority of relevant studies have been restricted to undrained wetland soils or those overlain by a thin peat layer (e.g., Trettin et al. 1997). Furthermore, even though nutrient dynamics of drained peatland forests have been quite thoroughly studied (e.g., Laiho et al. 1999), investigations of the nutrient status in planting spots, least of all of the prepared type, on thick-peated soils are lacking. Soil preparation is believed to accelerate nutrient release from OM (e.g., Kaunisto and Päivänen 1985, Londo and Mroz 2001), which presumably would be beneficial for seedling growth also on thick-peated sites. The soil carbon-to-nitrogen (C:N) ratio is an often used index of OM quality, and generally the higher the ratio, the more the N released during decomposition is immobilized by soil microbes (e.g., Enriquez et al. 1993). This could lead to N deficiency in seedlings and consequently limit growth.

Despite the apparent benefits of mounding, it is not a methodological panacea for peatland forest regeneration. Desiccation of mounds during prolonged dry periods and the infamously slow rewetting process of *Carex* peat mounds have been noted (Saarinen 1997, 2005). On sites with a thick peat layer, mounds lack a mineral soil component. Depending on the specific technique used, the peat mass may be inverted directly upon the excavated spot or beside the ditch (or pit) from which it was excavated. In the latter case, the spoil is placed on the intact peatland surface. Independent of the technique used, the mound bottom is typically comprised of an upturned humus layer, which is topped by more or less decomposed peat. Although peat mounds provide adequate substrate for Scots pine seedling establishment and growth during moist growing seasons, drought can radically impact regeneration success (Saarinen 2005). Hence, increasingly drier and hotter summers would clearly enhance the susceptibility of seedlings growing in peat mounds to drought.

The silvicultural basis for preparing soil is to thus advance tree seedling establishment and growth, and in forestry-managed peatlands these ends are presumably most reliably achieved by mounding prior to planting (Mannerkoski 1975, Kaunisto 1984). In addition to the silvicultural aspect, however, other important factors also come into play when considering which soil preparation method is most appropriate in a given situation. Mounding, which is an intensive form of soil preparation, is not necessarily the most cost-effective alternative on nutrient-poor forestry-drained sites. Site productivity must be weighed against regeneration costs. Hence, an alternative soil preparation method that is equally effective but more economical than mounding is paramount for practicing forestry especially on “marginal” sites. Moreover, there are also environmental and

climatic considerations. Mounding preceded by clearcutting on drained pine-dominated peatlands of low productivity has been found to severely diminish surface water quality via suspended solids, nitrogen, and phosphorus leaching (Nieminen 2003). Ditch mounding, wherein 40–60-cm-deep ditches at 12–25 m intervals are excavated concurrently with mounding, was deemed to endanger outflow water quality considerably more than mounding without shallow ditching. Furthermore, it has been suggested that peat mounds may release considerably more CO<sub>2</sub> into the atmosphere as a result of peat oxidation and heightened decomposition within them, and should this prove true, it may have climatic implications (Minkkinen et al. 2008). The extent to which soil preparation will affect the decomposition of OM will however depend on the amount of area disturbed as well as the severity of the disturbance to the OM (Bulmer et al. 1998, Prescott et al. 2000). All of these factors have the potential to undermine the suitability of mounding when regenerating forestry-drained peatland forests in the future.

On low to moderate fertility forestry-drained peatlands, which are also typically characterized by a thick peat layer, planting Scots pine seedlings in mounds after clearcutting is according to Finnish silvicultural recommendations for drained peatlands (Hyvän metsänhoidon... 2007) the safest and quite often also the cheapest regeneration solution in the long run due to the variability of weather conditions and the suckering of pubescent birch in regeneration areas. But what are the potential alternatives to mounding? One option is scalping, which involves scraping off the ground vegetation and humus layer in order to bare the underlying peat surface in patches. In the technical follow-through, it is especially important that the peat layer itself remains undisturbed and that depressions are not created in the soil surface (Hyvän metsänhoidon... 2007). Ditch maintenance is also advisable concurrently with scalping. Saarinen (2005) has reported promising results with excavator-based scalping in association with natural and artificial seeding of Scots pine on low to moderate fertility drained peatland sites. However, rainy growing seasons and/or a substandard drainage regime may endanger regeneration in scalps (Paavilainen and Päivänen 1995, Saarinen 1997). The least intensive alternative, doing nothing at all to the soil, is recommended only in rare instances when regenerating Scots pine naturally in the poorest sites having sufficient *Sphagnum* moss cover and thus good receptivity for seed germination. Notably, planting Scots pine is not recommended without preparing the soil first on forestry-drained peatlands (Hyvän metsänhoidon... 2007).

Thus far, published studies investigating the legitimacy of scalping and no mechanical site preparation as options in forestry-drained peatlands are relatively few, and experiences related to their application in peatland forestry at the practical level are also limited. Although both Mannerkoski (1975) and Kaunisto (1984) reported better survival and growth of Scots pine outplants in mounds versus unprepared microsites on drained, clearcut peatlands, a few studies also refute the superiority of mounding compared to leaving the peatland surface intact with lodgepole pine (*Pinus contorta* Dougl.) (Hendrick 1984), tamarack (*Larix laricina* (Du Roi) K. Koch) and black spruce (*Picea mariana* (Mill.) BSP) (Takyi and Hillman 2000). Rothwell et al. (1993) as well as Roy et al. (1999) emphasized the influence of planting spot selection on conifer seedling survival and growth on drained peatland sites with an undisturbed soil surface. In light of the stand replacement boom on forestry-drained peatlands in Finland, comparisons concerned with the feasibility of different soil preparation methods followed by reforestation especially on thick-peated, forestry-drained sites are grimly lacking.

### 1.3. Seedling tolerance to desiccated as opposed to waterlogged peat soil

Leaf yellowing or wilting, retarded growth, and physiological upset (e.g., in photosynthesis, water flow into roots) are common responses in trees to water stress (Kozłowski et al. 1991). Just as too little soil water poses a health risk to seedlings, too much water can be equally as debilitating. Strangely, both soil drying and flooding can be the cause of leaf dehydration (Kramer and Boyer 1995, Aroca et al. 2012). The impact of drought or flooding on plant function will however depend on the duration, intensity, and timing (e.g., dormant versus growing season, periodicity of shoot and root growth) of the stress, plant species as well as its developmental stage (Kozłowski 1984). Although one of the main goals of peat soil preparation is to manipulate soil water conditions for the benefit of seedlings, they may in fact experience heightened susceptibility to desiccation or alternatively to flooding in the face of extreme weather depending on the soil preparation method employed and peat properties. Thus, seedling tolerance to moisture-related stress is an important determinant of regeneration success. Concretely, the ability to withstand surplus moisture in scalps and water shortage in mounds is key, as these are likely scenarios to be increasingly encountered in the future due to climate change (IPCC 2007).

In peat soils, a minimum air space of 10% soil volume is considered critical for normal root development and plant growth (Päivänen 1973). If the volume of air is lower than this, then poor aeration becomes a growth-limiting factor. On the opposite end of the extreme, a volumetric water content of approximately 10–25% in peat soil represents the lower limit of available water to plants (Päivänen 1973). Kaufmann (1968) demonstrated in drying mineral soil that a soil water potential of  $-0.6$  to  $-0.7$  MPa ( $-600$  to  $-700$  kPa) encumbered root growth in Scots pine seedlings to a rate of only 25% of that in non-limiting conditions. As soil dries, soil water increasingly moves from capillary pore space and adheres to soil particles, hence making it, harder for plant roots to draw water from the soil. In general, the less decomposed the peat is, the greater its porosity, i.e., the greater the amount of space occupied by water and/or air and the greater the share of large-sized pores. Hence, while poorly decomposed peat contains a considerable amount of water at saturation, approximately 97% of volume, it releases it more easily under tension (as matric suction increases), for instance, as the soil dries. More decomposed peat, on the other hand, contains less water at saturation due to lower porosity and smaller pores, but the loss of water as the soil dries is comparatively smaller. The stage of decomposition correlates with bulk density, which is the oven-dry mass divided by the volume of the undisturbed, saturated peat sample (Päivänen 1969). For Finnish peats, bulk density typically ranges from  $0.04$  to  $0.20$  g cm<sup>-3</sup> (Päivänen 1973). Consequently, the bulk density of peat strongly influences its ability to retain water under drought conditions and in effect “regulates” the manifestation of drought stress in peat-grown plants.

Scots pine is a versatile conifer inhabiting both dry and wet environments from sandy upland soils to waterlogged organic ones. While some of the mechanisms Scots pine employs for dealing with extremely dry or wet conditions during the growing season may be similar (e.g., stomatal closure), there is also evidence of differing mechanisms of adaptation. For instance, while drought has been shown to clearly reduce seedling root and shoot growth (Kaufmann 1968, Rikala and Puttonen 1988, Otronen and Rosenlund 2001), Scots pine seedlings subjected to flooding have demonstrated considerable tolerance with little or no impact on growth at least in the short term (Zaerr 1983, Otronen and Rosenlund 2001, Mukassabi et al. 2012). Typically, the assessment of seedling vigor in field conditions such as that done in regeneration surveys and studies relies on morphological indicators, i.e., on what can be seen with the naked eye such as terminal shoot length and needle discoloration. Thus, the underground sphere harboring seedling root systems is often overlooked even though roots are the first plant organs to be in contact with dry or water-

logged soil. In instances where reduced vigor is observed, identifying the cause is not so simple, particularly when the time elapsed between planting and surveying is at least a few years. While seedling morphological traits are important to consider as they provide information on carbon allocation strategies under stress, a more complete picture may be gained with a multifaceted approach to interpreting seedling stress.

Though reduced growth is the outcome, i.e., the visible symptom of stress, it provides little information on how the plant responds at the onset of stress and as the stress progresses not to mention the precise mechanisms for dealing with it, which may be stage dependent. Paradoxically, a lack of visible symptoms is no guarantee of the absence of internal turmoil. Physiological changes due to stress, for example, in the efficiency of photosynthesis can potentially be detected before morphologically visible signs even appear (Maxwell and Johnson 2000). Chlorophyll fluorescence—a measure of photochemical efficiency—is indicative of the ability of a plant to tolerate stress as well as the extent of damage incurred by the photosynthetic apparatus in response to stress (Mohammed et al. 1995, Maxwell and Johnson 2000). Roots have a critical role in the defense against water-associated stress, for decreased movement of water into roots is a typical response of stressed plants (Kramer and Boyer 1995). While the size of the root system and number of fine root tips are key to plant water uptake under soil water stress, absorption is also affected by the colonization of root tips by symbiotic fungi, ectomycorrhizae (Cudlin et al. 2007). Furthermore, plant metabolism is known to be influenced by stress. Polyamines (PA), which are organic compounds commonly occurring in plant cells (Martin-Tanguy 2001), are recognized as being crucial in a plant's defense against abiotic stresses (Alcázar et al. 2010). Notably, PA concentrations are affected by drought stress in some plant species (Capell et al. 2004, Kasukabe et al. 2004, Ma et al. 2005).

Only by studying the coping strategies of Scots pine seedlings exposed to drought and waterlogging can we improve soil preparation methodology to better suit Scots pine regeneration on thick-peated soils in an uncertain climate. Sooner or later Scots pine seedlings outplanted in regeneration areas will confront a water shortage or surplus. But which perchance is the lesser of two evils?

#### **1.4. Potential impacts of peatland forest regeneration activities on greenhouse gas (GHG) emissions**

Human activities have increased atmospheric concentrations of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O), thus contributing to the greenhouse effect and climate change, which has aroused worldwide concern. Although CO<sub>2</sub> is the major driver behind global warming since it exists in much greater concentrations in the atmosphere, CH<sub>4</sub> and N<sub>2</sub>O trap more heat per mass unit, being respectively 25 and 298 times more potent greenhouse gases than CO<sub>2</sub> over a 100-year time span (IPCC 2007). Organic matter accumulation occurring over thousands of years makes peatlands huge stores of soil carbon. Pristine peatlands are generally sinks of CO<sub>2</sub> and high sources of CH<sub>4</sub> while emitting insignificant amounts of N<sub>2</sub>O. Disturbance to peatland such as through forestry drainage alters its natural hydrology and consequently greenhouse gas dynamics (Minkkinen et al. 2008).

Drainage lowers the WTL, which via improved aeration results in peat oxidation, compaction, and subsidence (Minkkinen and Laine 1998). Thus, accelerated decomposition of the formerly waterlogged peat leads to increased CO<sub>2</sub> emission into the atmosphere. Drainage also leads to



vegetation changes as mire species are replaced by forest species, which eventually affect the quantity and composition of litter production and therefore the carbon input into the soil (Laiho et al. 2003, Straková et al. 2010). As woody species become more abundant, the lignin content of litter tends to rise relative to more readily decomposable sugars and starches (Straková et al. 2010). Due to the recalcitrant nature of lignin, litter decay is retarded (Taylor et al. 1991, Straková et al. 2012). In addition, drainage reduces soil temperature and site pH (Laiho 2006) as well as increases the frequency of drought episodes afflicting the peat surface in the long run. All of these factors have a negative impact on decay rates (Laiho 2006, Straková et al. 2012).

At the same time, methane emissions markedly decrease because methanogenesis demands an anaerobic environment, i.e., the water-saturated layer lying below the water table (Martikainen et al. 1995). Drainage increases the thickness of the oxygenated surface peat layer, which not only enhances oxidation of  $\text{CH}_4$  but gradually evicts mire vegetation, thus more or less halting the input of carbon into the anoxic layer. The change, however, is smallest in nutrient-poor sites, which generally remain sources indeterminately (Minkkinen et al. 2008). Though drainage improves the capacity for nitrification due to increased mineralization through decomposition,  $\text{N}_2\text{O}$  emission from peat soils is regulated by aerobic nitrification and anaerobic denitrification processes, which again are influenced by site nutrient and oxygen status (Martikainen et al. 1993, Regina et al. 1996). Despite the large nitrogen pool in peat, it is mainly bound up in organic compounds, thus the availability of inorganic N constrains  $\text{N}_2\text{O}$  production. Therefore, drainage increases  $\text{N}_2\text{O}$  emission only from fertile peatland sites whose pH encourages nitrate formation (Martikainen et al. 1993, Regina et al. 1996).

Although the effects of drainage on soil  $\text{CO}_2$ ,  $\text{CH}_4$ , and  $\text{N}_2\text{O}$  fluxes within boreal peatland forests are well documented (e.g., Roulet et al. 1993, Martikainen et al. 1995, Silvola et al. 1996, von Arnold et al. 2005, Minkkinen et al. 2007, Ojanen et al. 2010) and the implications of clearcutting have also been investigated (Nieminen 1998, Huttunen et al. 2003, Saari et al. 2009, Mäkiranta et al. 2010, 2012), the commonly applied silvicultural measure of soil preparation has received little attention. Potentially, disturbance of peat soil through mechanical preparation may profoundly influence soil processes involved in the production and release of greenhouse gases. Improved aeration and warmer soil temperatures resulting from soil preparation could conceivably lead to accelerated rates of peat decay, especially when applying an intensive method such as mounding. In addition, watering up of the regeneration site caused by clearcutting (Heikurainen and Päivänen 1970, Marcotte et al. 2008) may revive  $\text{CH}_4$  production and emission. For instance, poor drainage efficiency in forested nutrient-poor sites has led to more or less similar  $\text{CH}_4$  emission rates as in pristine sites (Ojanen et al. 2010). Just how soil preparation would fit into this scheme is entirely unknown. Drier, prepared microsites like mounds would presumably microbially oxidize  $\text{CH}_4$  into  $\text{CO}_2$ , but moister scalps may provide a pathway for  $\text{CH}_4$  diffusion. Neither mounding nor scalping removes all the vegetation in an area, rather mounds and scalps alternate with a network of vegetated, outwardly intact microsites. Possibly, these latter mentioned could be impacted “indirectly” by the soil preparation maneuver. Although  $\text{N}_2\text{O}$  emissions from forestry-drained, pine-dominated peatlands are knowingly minimal, felling and consequent input of N from slash may nonetheless enhance  $\text{N}_2\text{O}$  formation even in poorer sites (Mäkiranta et al. 2012). Again, an information void exists as to the role that soil preparation might play in this context.

In light of the aforementioned, a clear need exists for investigating the GHG response of peatlands used in commercial forestry to silvicultural practices. Particularly, we are confronted with an immense gap in our present knowledge regarding how boreal, forestry-drained sites underlain by a thick peat layer respond to soil preparation. By filling this gap, the accuracy of estimations regarding the GHG balance at the national level is improved while the predicted impacts on

the atmosphere are better founded. Any harmful effects on the atmosphere will also have to be recognized in mitigation efforts, and in worst case, may constrain the range of feasible soil preparation methods that can be applied in peatland forestry. Hence, we are faced with a question of balance: How can we achieve sufficient regeneration results from the forestry aspect with the least detrimental effects on the atmosphere?

## 1.5. Aims

Soil preparation after clearcutting drained peatland sites modifies soil water and aeration conditions in order to promote tree seedling regeneration. While preparation of peat soil has other important benefits, like reducing competition with ground and field vegetation, the soil water status of created microsites is of principal concern for the establishment and early development of seedlings on peat substrate. Extreme weather events such as drought and abundant rainfall are known to impact the soil water status of elevated mounds and flat scalps composed of peat, respectively, thus potentially provoking stress reactions in seedlings. Such events are only expected to increase in frequency in the future due to climate change, hence the capability of seedlings to deal with drought and waterlogging stress is essential as is understanding their tolerance strategies. At the same time, preparation of the peat may very well alter the soil decomposition process in addition to those processes controlling  $\text{CH}_4$  and  $\text{N}_2\text{O}$  production and emission. Accordingly, these potential climatic impacts demand investigation. Any tendency of drying or waterlogging in prepared microsites induced by mounding or scalping would likely prompt fluctuations in gas fluxes, which would differ from undisturbed (“unprepared”) microsites. Thus, soil moisture—a lack or surplus of it—is the thread that binds this dissertation together.

In the following, a compromise between forest regeneration practices and greenhouse gas emissions is sought in order to improve the scientific and climatic basis for formulating silvicultural recommendations for drained peatland forests in commercial use. The physical environment of interest is low to moderate fertility, forestry-drained sites having a thick peat layer, which have been dominated by Scots pine prior to clearcutting, ditch maintenance, soil preparation, and planting with Scots pine seedlings. Specifically, the aims are to:

- 1) Elucidate the effects of peat soil preparation of varying intensity—scalping and mounding (low and high intensity mechanical disturbances)—as opposed to no soil disturbance (unprepared) on early regeneration success of planted Scots pine seedlings and the factors involved with special emphasis on the hydrological aspect (Study I).

- 2) Describe morphological, physiological, and metabolic responses of Scots pine seedlings to stress caused by soil drying and waterlogging in genuine peat soil, evaluate respective tolerances, and implications for regeneration success (Studies II and III, Summary).

- 3) Determine the short-term impacts of soil preparation on organic matter decomposition expressed as the  $\text{CO}_2$  emission from peat alone,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  dynamics, and identify the environmental drivers involved with particular focus on microsite water relations (Study IV).

- 4) Evaluate the pros and cons of mechanical preparation (mounding, scalping) versus no preparation of peat soil—silvicultural and climatic perspectives, potential methodological modifications, and practical recommendations.

## 2. MATERIALS AND METHODS

### 2.1. Experimental design for studying regeneration success

#### 2.1.1. Field site and treatments

In order to evaluate Scots pine regeneration success (Study I), a field experiment was established at Joenvarsisuo peatland, in Hyytiälä, Juupajoki municipality, Western Finland (61°50'41"N, 24°17'19"E). According to the Finnish classification system, the site represented a transitional form between dwarf shrub (Vatkg) and *Vaccinium vitis-idaea* (Ptkg II) drained peatland site types (Vasander and Laine 2008). Its moderately decomposed *Carex-Sphagnum* peat deposit exceeded 1.5 m. This 6-hectare riverside site had undergone initial drainage in 1933, ditch maintenance in 1986 (Sarkkola and Päivänen 2001), and clearcutting (stand volume 155 m<sup>3</sup> ha<sup>-1</sup>) in March 2006 followed by concurrent measures of ditch maintenance and soil preparation the subsequent autumn. Both applied methods of soil preparation, scalping and pit mounding, were excavator-based. Neither of these methods disrupts the peatland surface entirely, rather prepared microsites alternate with those still bearing vegetation (i.e., unprepared). During pit mounding, the digger bucket was thrust into the ground 25–30 cm, then dragged approximately half a meter simultaneously gathering soil, and finally, by means of its hydraulic flap, flipping over and compacting the peat mound atop unprepared ground next to the excavated pit. This technique left the deeper, excavated peat exposed and compacted on top of the mound and the original vegetated surface buried underneath. In effect, mounding produced two types of prepared microsites, mounds and pits. Scalping resulted in discontinuous patches of exposed peat from which the humus layer and vegetation had been removed.

The experimental area was divided into two approximately 0.3 ha blocks based on their apparent differences in moisture regime as evidenced by greater soil sogginess, sensitivity to flooding, and prevalence of mire as opposed to forest vegetation in the Northend versus the Southend (Study I, Fig. 1). Each block consisted of three 30 × 30 m treatment plots, i.e., scalping, pit mounding, and control plots. The soil in control plots was undisturbed with the exception of logging trails resulting from the clearcutting operation. The assortment of microsite types and their properties within each treatment are pictured in Study IV, Fig. 1. In May 2007, the site was planted with year-old containerized Scots pine (*Pinus sylvestris* L.) seedlings at a density of 2000 seedlings ha<sup>-1</sup>. The planting density was the same in all 6 treatments plots irrespective of the presence of naturally regenerated seedlings. Only prepared microsites were planted within the scalped and mounded plots. Seedlings were planted atop mounds and where applicable at the higher end of scalps, but pits were not planted since they were only a by-product of the mounding maneuver. For a more in-depth site description, refer to Studies I and IV. Please note that block–treatment plot are terminologically synonymous with the site–subsite designations used in Study I.

#### 2.1.2. Measurements

A regeneration survey was carried out at the end of the third growing season after outplanting. The survival, growth, and vitality of the 4-year-old seedlings on all six plots (2 blocks × 3 treatments) were assessed by means of circular fixed-area sampling. The density of living seedlings, their height and the length of their current-year terminal leader shoots were measured. In addition, the external vitality (i.e., outward appearance), as well as cause and incidence of



damage, if any, were determined for all seedlings found dead or alive. (Note: Not all of the perished seedlings could be located.)

### 2.1.3. Statistical analysis

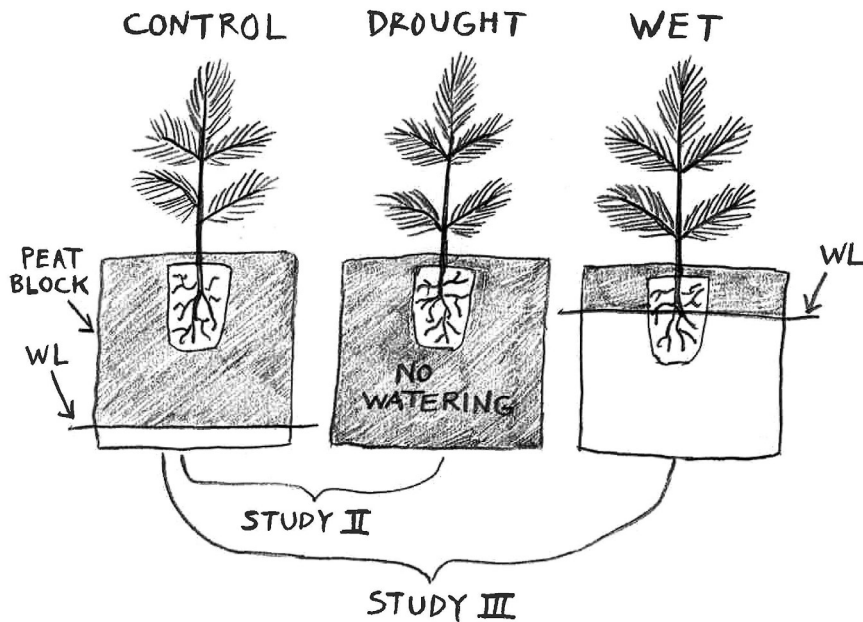
A general linear mixed model (Mixed procedure in the SPSS 17 statistical software package) with restricted maximum likelihood (REML) estimation method was used to test the effects of treatment and block on seedling survival rate, current-year terminal leader shoot length, and total height (see Study I, Section 2.6 for complete description of analysis).

## 2.2. Experimental design for studying seedling tolerance to drought and waterlogging stress

### 2.2.1. Greenhouse experiments and field sites

Guided by objective 2, both greenhouse and field experiments were set up. The first greenhouse experiment (Study II), which lasted from mid-June to mid-October 2008, focused on tolerance to drought stress whereas the second one (Study III) extended from late May to early September 2009 and dealt with tolerance to both drought and waterlogging. Both greenhouse experiments were carried out at the Finnish Forest Research Institute in Parkano, Finland (62°00'35"N, 23°01'30"E). The peat substrate and seedling material used in the controlled conditions of these two experiments matched those customary to peatland forestry. The seedlings grew outside in a lean-to with a transparent roof (i.e., makeshift greenhouse), and were thus sheltered from the rain. In Study II, seedlings in the drought treatment had to be moved indoors to the heated, greenhouse proper (situated beside lean-to) at the end of August in order to accelerate the soil drying process.

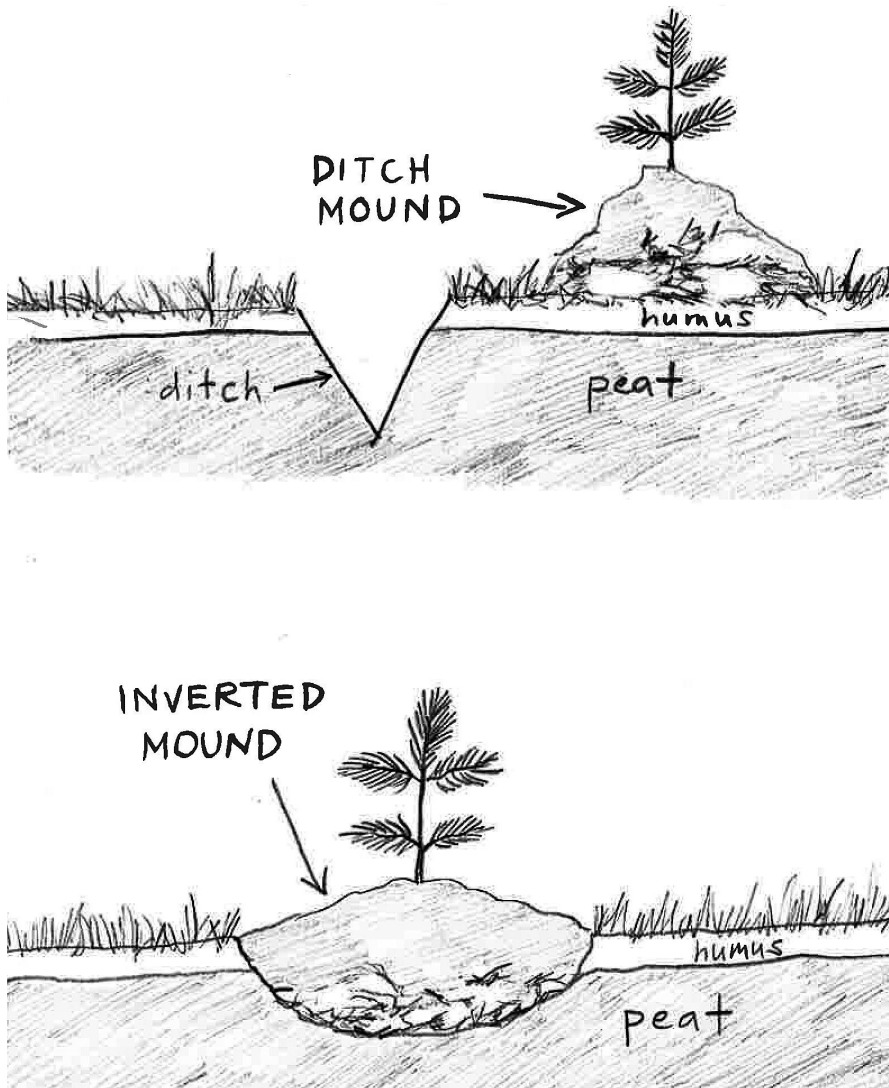
In the first greenhouse experiment (Study II), fifty 25 × 20 × 20 cm blocks of authentic, undisturbed highly decomposed *Sphagnum-Carex* peat were manually extracted (Study II, Fig. 1) from the drained Joenvarsisuo peatland described in Section 2.1.1. One-year-old containerized Scots pine seedlings were planted in the blocks. Half the seedlings represented the control and were placed in a PVC tub and watered from below. The other half rested on top of planks and were subjected to drought stress by withholding water entirely (Fig. 1). In the second greenhouse experiment (Study III), seventy-five 25 × 20 × 20 cm peat blocks were dug up from a dwarf shrub type (Vatkg) of drained peatland in Parkano. These blocks consisted primarily of poorly decomposed *Sphagnum* peat ("bottom"), but were topped by an approximately 5-cm-thick layer of *Sphagnum* peat ("surface"), which had decomposed moderately in response to drainage. Two-year-old containerized Scots pine seedlings were planted in the blocks. One-third of the seedlings represented the control treatment and were set in a PVC tub and watered from below. Another third of the seedlings were exposed to drought in the same manner as in the first experiment (Study II). The last 25 seedlings represented the wet treatment and were put in a PVC tub and exposed to an elevated water level for the duration of the experiment. The water level was maintained at approximately 6–7 cm below the top surface of the peat blocks, which meant the seedling pots were about halfway submerged (Fig. 1). Seedlings were never watered from above (i.e., on top of the soil) in either of the experiments, and the water level in the control treatment in both experiments was kept steadily at 18 cm below the top surface of the 20-cm-high blocks. This was considered sufficient to ensure capillary water movement and thus adequate moisture



**Figure 1.** General setup of greenhouse experiments (Studies II and III). In the control, the water level (WL) was maintained at 18 cm below the top surface of the 20-cm-high peat blocks. Water was withheld entirely from seedlings in the drought treatment. In the wet treatment, seedling pots were halfway submerged throughout. Seedlings were never watered from above. Each treatment contained 25 Scots pine seedlings (1 seedling per block) in both greenhouse experiments.

conditions throughout. In addition, the mean daily air temperature and relative humidity were recorded throughout each of the greenhouse experiments. At experiments' end, water retention at desorption (relative to wet volume at  $-0.3$  kPa) was determined from five, saturated, undisturbed fresh samples of the *Sphagnum-Carex* peat in Study II and separately for the surface and bottom components of the *Sphagnum* peat from five samples in Study III (Heiskanen 1993). The water retention curve indicates the level of suction required by the plant to draw water from the soil as it dries. Soil water increasingly moves from capillary pore space becoming bound to soil particles (adhesion), which consequently hinders plant water uptake.

In parallel to the second greenhouse experiment (Study III), two peatland sites, Haukilammenneva ( $62^{\circ}00'48''\text{N}$ ,  $23^{\circ}15'34''\text{E}$ ) and Häädetjärvi ( $62^{\circ}01'54''\text{N}$ ,  $22^{\circ}43'26''\text{E}$ ), located in Karttipärä and Laholuoma, Parkano municipality, Western Finland were selected for potentially observing drought and waterlogging stress in field conditions from late May to late August 2009. While Study III attempted to *mimic* the water-associated stress encountered by Scots pine seedlings in different mechanically prepared microsites on peat soil—desiccation of mounds versus waterlogging of scalps, the two field experiments provided the *real-world contrast* to controlled conditions. With this design, any “discrepancies” in the results on stress tolerance arising from the experimental environment—controlled versus often unpredictable field conditions—could be highlighted. Both sites represented the *Vaccinium vitis-idaea* (Ptkg II) drained peatland type and had a moderately decomposed *Sphagnum-Carex* peat layer exceeding 1 m in thickness. The Haukilammenneva site was drained in 1912, whereas the Häädetjärvi site in the 1950s. Both of



**Figure 2.** Two variations of excavator-based mounding applied at the Häädetjärvi experimental site. Ditch mounds were higher and drier than inverted mounds.

them were clearcut and their soil prepared in the autumn 2005. In addition, ditch maintenance was carried out concomitantly with soil preparation at the Häädetjärvi site.

The soil preparation method applied at the Häädetjärvi site consisted of two variations of excavator-based mounding: ditch mounding and inverted mounding (Fig. 2). In ditch mounding, spoil from the ditch being dug was dumped in heaps on the vegetated flanks of the ditch. In this case, the ditches were shallow, approximately 50 cm deep. The ditch mounds formed were typically 20–40 cm high. Inverted mounding involved digging up the soil in patches and turning the excavated soil mass upside down upon the same spot from which it was dug, hence leaving the

humus layer buried underneath (Fig. 2). This resulted in a patchwork of low mounds rising slightly above the peatland surface. Thus, no ditches were made in conjunction with inverted mounding. Conversely, excavator-based scalping was implemented at the Haukilammenneva site resulting in 35-cm-wide, 1–1.5-m-long bare peat patches from which the humus layer and vegetation had been removed. This scalping method corresponded to that applied at the Joenvarsisuo site (see Section 2.1.1.). In effect, a moisture gradient existed within both soil preparation treatments: dry vs. wet scalps *and* dry ditch mounds vs. moist inverted mounds. The categorization of scalps as either dry or wet was based on median water table data collected prior to 2009. In dry scalps, the median WTL ranged between 30–55 cm below the soil surface, and in wet scalps 12–20 cm. The Haukilammenneva experiment included 25 dry scalps (DS) + 25 wet scalps (WS). Accordingly, the Häädetjärvi experiment was composed of 25 ditch mounds (DM) + 25 inverted mounds (IM). At both sites, two-year-old containerized Scots pine seedlings were planted in these prepared microsites in May 2009. These seedlings originated from the same batch as those used in the 2009 greenhouse experiment (Study III). At the Häädetjärvi site, perforated PVC tubes for determining the WTL relative to the soil surface were installed beside each mound. The difference in elevation between the mound summit and installation point of the respective WTL tube was determined by leveling from a mutual reference point. WTL tubes had already been installed in scalps at the Haukilammenneva site. Furthermore, temperature loggers (iButton, Maxim, USA) were inserted to 5 cm depth in mounds (3 ditch + 3 inverted) and scalps (3 dry + 3 wet) and these continuously measured soil temperature every 2 hours. Air temperature and rainfall were not measured at these sites, thus the values presented later on are based on the Finnish Meteorological Institute's  $10 \times 10$  km weather grid system.

## 2.2.2. Measurements

### Chlorophyll fluorescence and soil water content

Chlorophyll fluorescence served as a diagnostic tool for monitoring the physiological status of needles repeatedly from the same seedlings as the level of stress increased. The most widely used chlorophyll fluorescence parameter in interpreting plant responses to environmental stress and as an indicator of photoinhibition is the ratio of variable to maximal fluorescence yield ( $F_v/F_m$ ), i.e., the maximum potential quantum yield of Photosystem II (PSII) (Öquist and Wass 1988, Mohammed et al. 1995, Maxwell and Johnson 2000). In describing the potential photochemical efficiency of PSII, an  $F_v/F_m$  value of approximately 0.83 is generally considered normal for healthy plants, and a sustained decline in  $F_v/F_m$  is indicative of plant stress (Maxwell and Johnson 2000).

Chlorophyll fluorescence was measured from detached previous-year ("old") needles and also from current-year ("new") ones once they had grown to measurable size. One new needle from the current-year leader shoot and one old needle from the previous-year leader shoot per seedling were plucked with tweezers approximately midway up the respective shoots between 08:00–09:00, placed in a plastic bag, and stored in a small cooler to await darkening and measurement within 6 hours. After collection, 20 sampled needles at a time were dark adapted for half an hour in leaf clips equipped with a shutter plate inside a black, light-impenetrable bag at room temperature 20°C. Thereafter, the  $F_v/F_m$  parameter was derived from the induction kinetics of chlorophyll fluorescence using the non-modulated Plant Efficiency Analyzer (Hansatech Instruments Ltd., U.K.) with its probe set at 100% of maximum light (i.e., saturating) intensity for 15 seconds. The probe's six light-emitting diodes (LEDs) illuminate the leaf surface with

red light having a peak wavelength of 650 nm. Thus,  $F_v/F_m$  = photochemical trapping efficiency in the dark-adapted state, i.e., the maximum potential quantum efficiency of PSII if all capable reaction centers were open.

Chlorophyll fluorescence was measured from all seedlings approximately every 5–10 days in both greenhouse experiments (Studies II and III), and about every second week at the two field sites. On the same occasions, the volumetric water content (WC, %) of the peat substrate was measured using a soil moisture meter equipped with a sensor (Moisture Meter HH2 and ThetaProbe ML2x, Delta-T Devices Ltd., U.K.). The sensor bears four, 6-cm-long spikes, which are inserted into the soil. Typically, four spots around each seedling were measured to attain the mean soil WC. Additionally at the two field sites, the WTL in prepared microsites was measured by inserting a battery-operated, water sensitive rod into the respective PVC tube.

### Polyamine analysis

In both greenhouse experiments (Studies II and III), concentrations of the PAs putrescine, spermidine, and spermine in different organs of the seedlings were analyzed to study the impact of water-related stress on seedling metabolism. In the drought-only experiment (Study II), current- and previous-year needles and fine roots from four seedlings per treatment at four different stages of the experiment were sampled (100–400 mg fresh mass (FM) per sample) for determining free and soluble conjugated PAs (2 treatments  $\times$  4 seedlings  $\times$  3 organs  $\times$  4 sampling occasions = 96 samples). In the second experiment dealing with drought and waterlogging stress (Study III), free PA concentrations in current-year needles, shoots, and fine roots were analyzed once from five seedlings per treatment at the end of the experiment (3 treatments  $\times$  5 seedlings  $\times$  3 organs = 45 samples). Samples were processed, stored, and analyzed according to standard procedures including the use of high-performance liquid chromatography (HPLC) (Sarjala and Kaunisto 1993, Fornalé et al. 1999).

### Root and shoot characteristics

At the conclusion of the greenhouse and field experiments, seedlings were examined to characterize their root and shoot traits. The specific traits measured varied between experiments, although the same traits were indeed measured in both field experiments. This approach was viewed appropriate for charting the diversity of morphological responses to water-associated stress in Scots pine.

In Study II, four seedlings per treatment were selected from which the following traits were characterized: 1) dry biomass (DM) of shoots and roots; 2) water content of shoots and roots; 3) root-to-shoot ratio; 4) total number of living and dead (*defunct*) fine root tips; 5) proportion of fine root tips colonized by ectomycorrhizae; 6) number of living fine root tips  $\text{mg}^{-1}$  root DM. Prior to microscopic examination of the roots, the FM of the roots and shoots was determined. The root samples were cleaned and segmented into suitable portions for viewing under the microscope. Roots tips appearing dark, flat, damaged, and/or lifeless were collectively classified as *defunct*. Thereafter, the roots and shoots were dried in an oven at 105°C overnight and then reweighed.

In Study III, five different shoot traits were measured from all of the seedlings as follows: 1) seedling height; 2) length of the current-year terminal leader shoot; 3) diameter (D) at midsection of the current-year terminal shoot; 4) D of previous-year terminal shoot; 5) apical bud length. In addition, five seedlings per treatment were sampled to determine 6) current-year needle length and 7) FM, and 8) FM of the terminal bud group. Items 6 and 7 were based on 20 new needles



removed from the current-year terminal shoot of each sampled seedling (20 needles  $\times$  5 seedlings  $\times$  3 treatments). Regarding the measurement of root traits, four seedlings per treatment were selected for determining root hydraulic conductance ( $K_r$ ).  $K_r$  ( $\text{kg s}^{-1} \text{MPa}^{-1}$ ) was measured with a high pressure flow meter (HPFM, Dynamax Inc., Houston, TX) (Tsuda and Tyree 2000). Afterwards, roots were separated from the soil and their length, surface area, and projected area (i.e., volume) determined by scanning (WinRhizo, Régent Instruments Inc., Québec, Canada). Root hydraulic conductivity ( $L_p$ ), i.e., the water flow rate per unit pressure scaled by root volume (RV) or surface area (RA), was obtained by dividing  $K_r$  by RV ( $\text{kg s}^{-1} \text{MPa}^{-1} \text{cm}^{-3}$ ) and RA ( $\text{kg s}^{-1} \text{MPa}^{-1} \text{cm}^{-2}$ ). For the sake of simplicity, the mass unit in  $K_r$  and  $L_p$  has been converted to mg in applicable figures and tables. Lastly, the roots were dried in an oven at  $105^\circ\text{C}$  overnight and weighed to determine DM. Altogether eight different root traits including conductance were analyzed: 9) RA; 10) RV; 11) length of fine roots; 12) length of all roots; 13) DM; 14)  $K_r$ ; 15)  $L_{p(\text{RV})}$ ; 16)  $L_{p(\text{RA})}$ .

At the Haukilammenneva and Häädetjärvi sites, all 100 seedlings were examined 15.–16.9.2009 to determine 1) height, 2) length of current-year terminal leader shoot, 3) external vitality (same classification used as in Study I) and any possible cause and type of damage. Thereafter, every fifth seedling was lifted in its entirety and bagged, then stored in a freezer until processing (2 microsite types  $\times$  2 soil moisture levels  $\times$  5 seedlings = 20 seedlings). Once thawed, stems were severed at the root collar, root systems were cleaned, and afterwards both portions were weighed (FM). They were then dried overnight at  $105^\circ\text{C}$  and reweighed to ascertain 4) DM of shoots and roots, 5) water content of shoots and roots, and 6) root-to-shoot ratio.

### 2.2.3. Statistical analyses

Irrespective of experiment, the analyses of the chlorophyll fluorescence parameter  $F_v/F_m$  and free polyamine concentrations (where applicable) were based on linear mixed models (procedure MIXED in SPSS 17, SPSS, Inc., Chicago, IL, USA). Treatment (T), needle age (N) (or sample type for polyamine testing), and time (D) were treated as fixed effects and seedling as a random effect. Model structures are described in greater detail in Studies II and III. The models define a split-plot structure with needle age (or sample type) as a split-plot treatment. A first-order autoregressive (AR1) covariance structure was assumed for the time correlation between the residuals of a needle age of a seedling. The Bonferroni adjustment method was applied to the confidence intervals and significance values to account for multiple comparisons. Variances of the residuals of the fluorescence parameter ( $F_v/F_m$ ) depend on the expected values and the fluorescence parameter values were transformed using an arcus sine square root transformation. In spite of the transformation, the variances of the residuals were dependent on the predicted values, which was taken into account by using regression weights  $w = 1/(\text{pred}_u * (1 - \text{pred}_u))$ , where  $\text{pred}_u$  is a predicted value computed by unweighted analysis. This, however, was not the case for the Haukilammenneva and Häädetjärvi datasets, which did not have to be weighted after applying the transformation. Normality and homogeneity of the variance of the residuals were checked graphically and the selection of the covariance structure was based on Akaike's information criteria.

Regardless of experiment, the distributions of all root and shoot characteristics were tested for normality and equality of variances before running one-way ANOVA to test the significance of the treatment effect using the same statistical package mentioned above. The Bonferroni method was used as the post hoc test for multiple comparisons. The level of significance applied in all testing was 0.05.

## 2.3. Experimental design for studying greenhouse gas fluxes

### 2.3.1. Field site and preparations for flux measurement

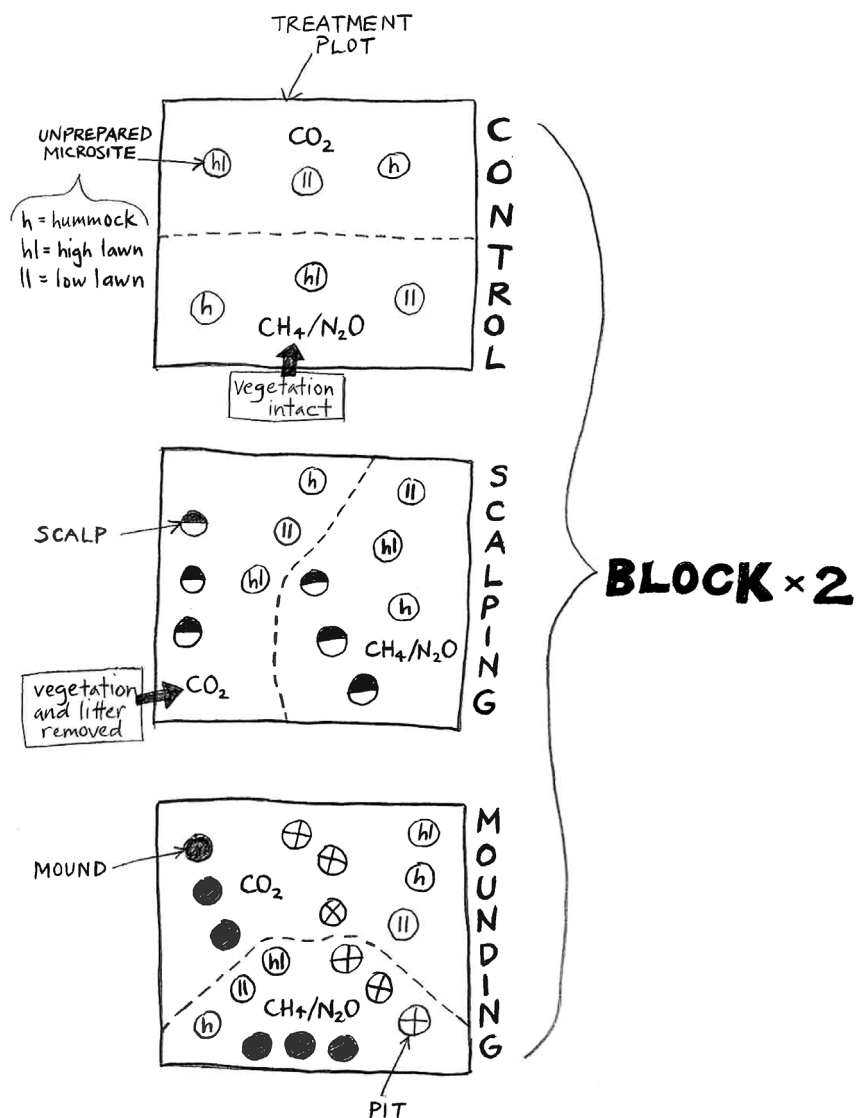
The Joenvarsisuo site described above in Section 2.1.1. served as the backdrop for quantifying the effects of soil preparation on CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O fluxes (Study IV). In the Northend and Southend blocks alike, microsites for gas measurement were randomly selected to represent the microtopographic features within each treatment. Furthermore, the experiment consisted of two separate sets of microsites for measuring 1) CO<sub>2</sub> and 2) CH<sub>4</sub>/N<sub>2</sub>O fluxes due to their differing geneses and dynamics. Study IV, Fig. 1 illustrates the principal types of microsites present in each treatment and Fig. 3 below depicts the experimental layout; 3 microsites of a given type per treatment were selected as subjects for measurement. For example, a mounding treatment plot included 3 mounds, 3 pits, and 3 unprepared microsites for measuring CO<sub>2</sub> (Fig. 3). In all treatments, the unprepared microsite type was represented by 1 hummock, 1 high lawn, and 1 low lawn (Fig. 3) (not indicated in Study IV, Fig. 1). All selected unprepared microsites were outwardly intact and entirely covered with living vegetation (100% of microsite surface area). Altogether 72 microsites were studied, half of which for quantifying CO<sub>2</sub> emissions and the other half for determining CH<sub>4</sub>/N<sub>2</sub>O flux rates.

To attain the decomposition rate of peat soil alone, all sources of plant respiration must be excluded. Hence, heterotrophic soil respiration ( $SR_p$ ) is the aerobic decomposition of soil organic matter by microbes (soil respiration – root respiration =  $SR_p$ ). Thus, in June 2007, the roots around CO<sub>2</sub> sample microsites were cut using a handsaw and thereafter an aluminum collar (Ø 31.5, A 780 cm<sup>2</sup>) with a 25-cm-long sleeve was shoved into the peat as a means of stifling production and respiration of new roots. The superficiality of most of the roots in peatlands (e.g., Laiho and Finér 1996, Finér and Laine 2000) justifies the trenching procedure as a means of suffocating root respiration. Furthermore, all aboveground organs of ground and field vegetation were excised and freshly fallen litter removed.

CH<sub>4</sub>/N<sub>2</sub>O microsites were likewise demarcated as described above in order to snugly set a short-sleeved (5 cm) collar into the ground, but otherwise vegetation within the collar was not impaired. Thus, unprepared CH<sub>4</sub>/N<sub>2</sub>O microsites remained fully vegetated throughout the experiment. Boardwalks were constructed around the sample microsites to avoid meddling with gas fluxes during measurements. Perforated PVC tubes for determining the WTL relative to the soil surface were installed beside the collared microsites. The difference in elevation between the microsite surface and installation point of the respective WT tube was determined by leveling from a mutual reference point. Temperature data loggers (iButton, Maxim, U.S.A.) were inserted into selected microsites to depths of 5 or 30 cm below the soil surface. The loggers recorded soil temperature every 2 hours in the summer and every 3 hours in the winter. Since soil temperature is an important environmental driver of  $SR_p$ , these logger-generated, continuous temperature data allowed us to simulate CO<sub>2</sub> fluxes throughout the study period.

Since the influence of cottongrass on the emission of CH<sub>4</sub> is well established (Schütz et al. 1991, Thomas et al. 1996, Tuittila et al. 2000), and it was especially abundant in our Northend block, the coverage of cottongrass in all 36 CH<sub>4</sub>/N<sub>2</sub>O microsites was determined once in September 2008.

The total surface area and percentual distribution of microsite types (prepared vs. unprepared) were determined for the 6 treatment plots (2 blocks × 3 treatments) by means of a line transect survey (Study IV, Table 1). Flux data was collected year-round from July 2007 through August 2009. Mean daily air temperatures from the first winter onwards and daily precipitation sums



**Figure 3.** Experimental design for measuring greenhouse gases fluxes from soil at the Joenvarsisuo drained peatland site. Each small circle represents an individual microsite. The dashed line separates  $\text{CO}_2$  microsites from those selected for  $\text{CH}_4/\text{N}_2\text{O}$  flux determination. The experiment (Study IV) consisted of 2 blocks (Northend, Southend) within which 3 treatments (control, scalping, mounding) were applied.

during snow-free periods are exhibited in Study IV, Fig. 2. Average monthly air temperatures and rainfall relative to long-term averages during the growing season are shown in Study I, Fig. 2. These data originated from the weather station at a nearby peatland situated 3.6 km further south from the Joenvarsisuo site.



### 2.3.2. Measurements

Throughout the CO<sub>2</sub> measurement campaign, sprouting vegetation was regularly snipped and newly deposited litter removed from the microsites. Soil CO<sub>2</sub> effluxes were measured weekly during the summer period (May–October) and monthly to bimonthly during the winter (November–April) by employing the closed chamber method (Alm et al. 2007). For this, a portable infrared gas analyzer attached via rubber hoses to a soil respiration chamber (Ø 31.5 cm, h 12.2 cm) was used (EGM-4 Environmental Gas Monitor for CO<sub>2</sub> + modified SRC-1 soil respiration chamber, PP Systems, UK). The metal chamber was placed on the collar groove of CO<sub>2</sub> sample microsites and the change in the CO<sub>2</sub> concentration over time (80–120 seconds) measured. EGM-4 automatically monitors the CO<sub>2</sub> concentration increase within the chamber headspace at 1.6 s intervals and calculates an average every 4.8 seconds. The soil CO<sub>2</sub> efflux (g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>) is thus based on the linear increase over time of the CO<sub>2</sub> concentration in the chamber.

Leaving vegetation in microsites intact, CH<sub>4</sub> and N<sub>2</sub>O fluxes were determined every 2–4 weeks in the summertime and monthly to bimonthly in the wintertime using the vented static chamber method (Alm et al. 2007). For gas sampling, a metal chamber (Ø 31.5 cm, h 29.8 cm) equipped with a fan and air temperature sensor was set on the collar in the same manner as in CO<sub>2</sub> measurements (Fig. 4). Over a 35-minute period, 4 gas samples were drawn from the chamber headspace via transfer tubes into 35 ml polypropylene syringes after 5, 15, 25, and 35 minutes had elapsed. CH<sub>4</sub> and N<sub>2</sub>O concentrations of gas samples were then analyzed in the laboratory within 2–3 days using a gas chromatograph equipped with FI and EC detectors. The respective gas fluxes were calculated based on the slope of the linear regression between gas concentration and measurement time (mg CH<sub>4</sub> or N<sub>2</sub>O m<sup>-2</sup> d<sup>-1</sup>).

When snow cover was present, a portable snowshoe collar (with sleeve sawed off to 10 cm) was used as an aid (Fig. 4). This consisted of a thin hexagonal piece of plywood hollowed from the middle upon which the sawed off collar rested and through which its short sleeve protruded. This device enabled gas measurement with limited disturbance to the snow cover atop the microsite. Whenever a microsite was flooded, an extension collar was set upon the stationary collar in the ground.



**Figure 4.** The vented static chamber method was employed to measure CH<sub>4</sub> and N<sub>2</sub>O fluxes from peat soil (Study IV). When snow cover was present, a “snowshoe collar” was used as a measurement aid. It consisted of a piece of plywood hollowed out from the middle and a short-sleeved collar. The chamber was set upon this apparatus in order to minimize disturbance to the snow layer and thus avoid altering the conditions of the measured microsite.

After each gas measurement event during the frost-free period, soil temperature at 5 and 30 cm depth was measured to the nearest tenth of a °C from the middle of each microsite with a TES-1312A digital thermometer with K type thermocouple input sensor (TES, Taiwan, R.O.C) and stainless steel temperature probe. These temperature data corresponded to those instances when fluxes were measured during the growing season (i.e., soil temperature precisely at the moment of gas measurement) and were used in creating the explanatory CO<sub>2</sub> efflux models necessary for simulation (see Study IV, Section 2.5). During the winter, however, soil temperature could not be measured in the same fashion due to soil frost, thus logger-based temperature data was used to correspond with winter flux measurements. In conjunction with gas measurement, the WTL to the nearest cm was recorded for each microsite and thereafter readings were corrected for microsite height (+) or depth (−). If a microsite was flooded, supersurface water depth was also measured.

At the conclusion of flux measurements, gravimetric peat soil samples (0–10 and 10–20 cm depth below microsite surface) were extracted from the middle of 18 microsites with a box-shaped peat corer. Since soil C:N ratio is most readily measured and frequently used as a predictor of decomposition rate (Chapin et al. 2002) and may consequently limit N availability to seedlings in their planting spots, it was the focus of the nutrient analysis (Study I). Thus, the analysis was limited to mounds, scalps, and unprepared microsites within the control treatment (i.e., “planting spots”) from which CO<sub>2</sub> fluxes were measured. All 36 samples were analyzed via CEM (HNO<sub>3</sub> + H<sub>2</sub>O<sub>2</sub>) (acid digestion for elemental analysis), ICP, and LECO CHN-2000 techniques for nutrient content based on dry mass (mg g<sup>−1</sup>).

### 2.3.3. Statistical analyses

Statistical analysis of flux datasets employed a general linear mixed model with restricted maximum likelihood (REML) estimation method (Study I) and a generalized estimating equation with gamma distribution and logarithm link function (Mixed and GEE procedures in the SPSS 17 statistical software package) (Study IV). Since soil preparation presumably influences soil temperature, aeration and moisture as well as substrate quality, the effects of treatment, block (*site* in Study I), time, and peat sample depth and their interactions (if applicable) on soil temperature at 5 cm depth (T5), WTL, C and N concentrations and C:N, and instantaneous summertime  $SR_p$  (g CO<sub>2</sub> m<sup>−2</sup> h<sup>−1</sup>) were tested (Study I). Thus, the MIXED analysis was performed on planted microsites only (scalps; mounds; unprepared microsites within control treatment) during the growing season (May–October 2007–2009) (Study I). In order to meet the assumptions of the statistical inference procedure in the MIXED model, a square root transformation for the dependent variable  $SR_p$  was applied.

In the GEE analysis, testing focused on whether or not soil preparation had a significant impact on instantaneous, year-round GHG emissions (g m<sup>−2</sup> h<sup>−1</sup>) from November 2007 through August 2009 (Study IV). The analysis encompassed all microsite types in all treatments. Namely, comparisons were made between: 1) control microsites (i.e., unprepared microsites in the control treatment plots), scalps, mounds, and pits; 2) unprepared microsites in the three respective treatments (control, scalping, mounding), i.e., treatment plots (consult Fig. 3 to visualize). Hence, the effects of the independent variables block, microsite type (in the case of comparison 1) *or* treatment (in the case of comparison 2), and time and their interactions (if applicable) on year-round instantaneous fluxes of CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O were tested. Instantaneous summer and winter flux values were processed together in the statistical runs.

In both the MIXED and GEE analyses, the differing hydrology of the blocks was of interest, thus block was treated as one of the factors in these models. However, independent replicates of the two block types were lacking. Consequently, different block–treatment (or block–microsite type) combinations did not have replicates, thus block\*treatment and block\*treatment\*time interactions could not be tested.

The Bonferroni adjustment method was applied to the confidence intervals and significance values to account for multiple comparisons of the estimated marginal means in all models. The level of significance applied in all testing was 0.05. On a separate note, simulated annual GHG fluxes (see next section) were not tested statistically for reasons specified in Study IV, Section 2.4.

#### 2.3.4. Flux modeling and simulation of annual emissions

In drained peatlands, soil temperature typically accounts for the majority of temporal variation in heterotrophic soil respiration (Mäkiranta et al. 2008). Temporal variation in temperature and CO<sub>2</sub> fluxes is high, and this dependence is usually non-linear. Therefore, to attain an unbiased estimate of CO<sub>2</sub> emissions over a longer period (e.g., growing season),  $SR_p$  must first be modeled and then simulated using measured temperature data. In creating the explanatory CO<sub>2</sub> model, the function proposed by Lloyd and Taylor (1994) was deemed most credible to describe the temperature dependence of  $SR_p$ . At this stage, soil temperatures recorded with the hand-held thermometer were used in modeling growing season fluxes, while interpolated temperature data from the loggers had to be used to model wintertime fluxes (Study IV). The model was as follows:

$$SR_p = R_{ref} \exp [E_0((1/(T_{ref} - T_0) - 1/(T_s - T_0)))] \quad (1)$$

where  $R_{ref}$  is the soil respiration rate (g m<sup>-2</sup> h<sup>-1</sup> of CO<sub>2</sub>) at reference temperature 10°C, when WTL is not limiting;  $E_0$  is an exponential parameter depicting the temperature sensitivity of soil respiration;  $T_{ref}$  is the reference soil temperature set at 10°C;  $T_0$  is the temperature minimum at which respiration approaches zero, -46.02°C; and  $T_s$  is the soil temperature at 5 cm depth measured concurrently with CO<sub>2</sub> efflux.

Model 1 was fitted separately to the datasets according to block (Northend, Southend), treatment (control, scalping, mounding), and microsite type (mound, pit, scalp, unprepared) using the nonlinear regression in SigmaPlot 11.0 (Systat Software, Inc., San Jose, CA, USA). The temperature dependence of  $SR_p$  was, however, generally much weaker in the Northend with  $r^2$  values often lower than 0.40 on account of the wetter conditions. Furthermore, soil temperature poorly explained  $SR_p$  in scalps and pits in both blocks when fitting the above model 1 to the corresponding datasets ( $r^2$  values at or below 0.20). Hence, using the multiplicative approach described by Riutta et al. (2007) for fens, a sigmoid WTL term was then incorporated into model 1 as follows:

$$SR_p = R_{ref} \exp [E_0((1/(T_{ref} - T_0) - 1/(T_s - T_0)))] \times 1/[1 + \exp(-(WTL - a)/b)] \quad (2)$$

where  $WTL$  is the depth (cm) of the water table measured concurrently with CO<sub>2</sub> efflux,  $a$  is the WTL at slope maximum, and  $b$  is the slope.

In both blocks, the most meaningful parameters were obtained with function 2 for unprepared microsites in all treatments and for mounds (Study IV, Table 3). In effect, blockwise functions for mounds and unprepared microsites in different treatments were then used to simulate hourly fluxes throughout the year and add up the annual CO<sub>2</sub> efflux (g m<sup>-2</sup> a<sup>-1</sup>). At this stage, continuous soil temperature (T5) data provided by the loggers and interpolated mean WTL values for respective microsite types served as the driving variables in flux simulation across the period November 2007–August 2009. *SR<sub>p</sub>* modeling for scalps and pits was unsuccessful due to the adverse effects of waterlogged soil. Therefore, their blockwise means were calculated from the instantaneous fluxes of the three corresponding microsites on each measurement occasion. Fluxes between these occasions were then interpolated to estimate their annual rates of *SR<sub>p</sub>*. Due to the reported initial effects of trenching on soil respiration (e.g., Bowden et al. 1993, Mäkiranta et al. 2008, 2010), wherein dying roots and fine root residues result in overestimation of soil respiration attributable to peat decomposition for a few months after the trenching procedure, we excluded data measured prior to November 2007 from these calculations (Study IV). The effects of trenching were namely apparent in Study I as instantaneous CO<sub>2</sub> fluxes peaked during the 2007 growing season (Study I, Fig. 6).

In the same manner as with CO<sub>2</sub> fluxes of scalps and pits, CH<sub>4</sub> and N<sub>2</sub>O fluxes between occasions of measurement were interpolated for all microsite types according to block and treatment from November 2007 through August 2009 in order to arrive at annual flux rates (g m<sup>-2</sup> a<sup>-1</sup>).

After computing annual greenhouse gas flux rates for each microsite type in a given treatment according to block, these values were weighted by their corresponding proportional surface area (%) within a given treatment plot (Study IV, Table 1 and Section 2.7). In doing so, the impact of each treatment (mounding, scalping, control) by block (Northend, Southend) on annual greenhouse gas fluxes could be attained. Thereafter, CH<sub>4</sub> and N<sub>2</sub>O flux rates were converted to their CO<sub>2</sub> equivalents over a 100-year time span (Global Warming Potential (GWP) 25 and 298, respectively) (IPCC 2007) and then combined with those for CO<sub>2</sub>. The short-term impacts of soil preparation versus no preparation on GHG emission in each block were thus ascertained.

### 3. RESULTS

#### 3.1. Regeneration success

After three growing seasons, the survival of Scots pine seedlings on peat soil was taxed the most in scalps (Study I, Fig. 7a and Table 4). Outplant survival in mounds, on the other hand, was far superior to scalps in addition to unprepared planting spots. Seedling survival did not differ significantly between the latter two mentioned treatments. Regarding height, seedlings planted in scalps were significantly shorter than in mounds and unprepared spots (Study I, Fig. 7b). Similarly, outplants in scalps also had significantly shorter current-year terminal leader shoots than those in the other two treatments (Study I, Fig. 7c). Notably, seedling height and growth in unprepared spots corresponded to those in mounds.

Of the planted seedlings found (*dead* or *alive*) within circular sample plots, the vitality displayed by those in scalps was silviculturally unsatisfactory (Fig. 5). Most of these seedlings were at best in a weakened state of health. Root suffocation due to waterlogged soil combined with foraging by the European pine weevil (*Hylobius abietis* L.) afflicted seedlings growing in scalps (Study I, Table 5). In unprepared spots, most of the seedlings found were in reasonably good health (Fig. 5) despite harassment by the pine weevil (Study I, Table 5). In mounds, seedlings typically appeared vibrant and healthy (Fig. 5). Mounding seemingly reduced pine weevil damage on peat soil relative to other treatments though it did not eradicate the problem (Study I, Table 5). Terminal leader damage was often evident in seedlings growing on mounds. This was likely due to browsing by grouse despite being classified as damage of an unknown source in Study I, Table 5. Overall, only a small minority (14%) of all the outplants surveyed had averted damage; this in itself epitomizes the challenge faced by reforestation efforts.

#### 3.2. Seedling tolerance to drought and waterlogging stress in peat soil

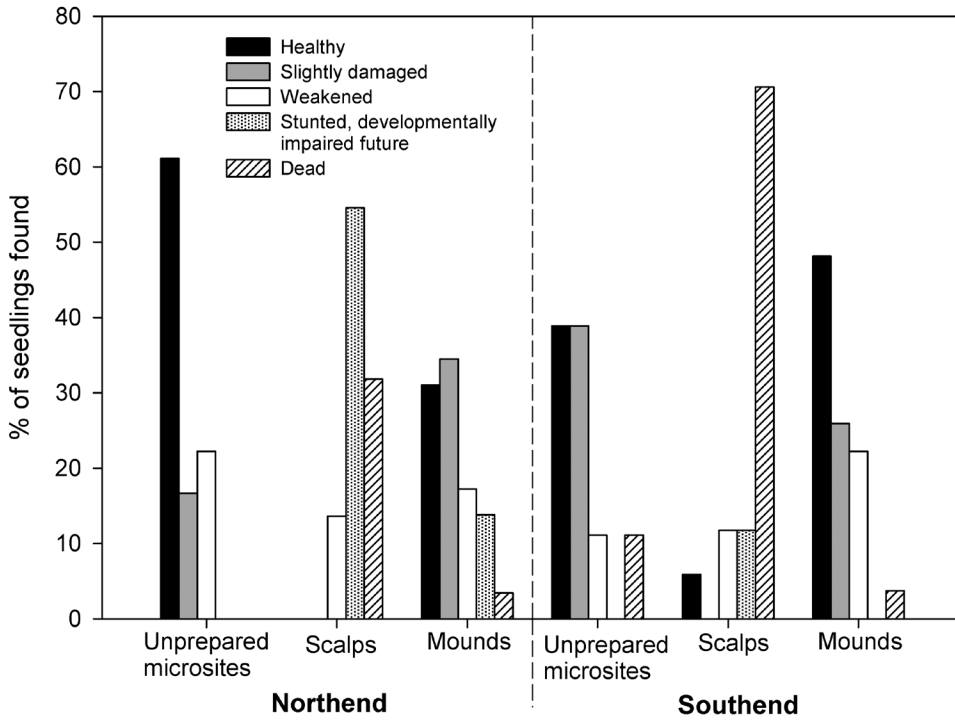
##### 3.2.1. Greenhouse experiment I: drought stress

##### Bulk density and water retention curve of peat substrate

The bulk density of the highly decomposed *Sphagnum-Carex* peat (dry mass to wet volume at  $-0.3$  kPa) amounted to  $0.22 \pm 0.03$  g cm<sup>-3</sup>. The estimated total porosity of the peat was  $85.53 \pm 2.20\%$  of soil volume, which is equivalent to the approximation made by Päivänen (1982) for peat in an advanced stage of decomposition. Water retention at desorption (relative to volume at  $-0.3$  kPa) is presented in Study II, Fig. 3 wherein the water availability distinctions at corresponding units of pressure have been modified from Päivänen (1973). In this particular peat, the permanent wilting point ( $-1554$  kPa, i.e., pF 4.2) (Taiz and Zeiger 1991) lay at a volumetric soil water content of approximately 28% (Study II, Fig. 3).

##### Soil water content and photochemical efficiency

Overall drought significantly lowered the photochemical efficiency ( $F_v/F_m$ ) of both old and new needles in Scots pine seedlings relative to the control (Study II, Table 1, Figs. 4 and 5). A significant three-way effect between treatment, needle age, and time was also found (Study II,



**Figure 5.** Vitality of planted Scots pine seedlings according to microsite type and block after three growing seasons at the forestry-drained, clearcut Joenvarsisuo site.

Table 1). The precise stages at which peat water content began to limit photosynthesis in old and new needles can be seen in Study II, Figs. 4 and 5, respectively. When the volumetric WC of the peat in the drought treatment had dropped to approximately 25–30%,  $F_v/F_m$  of old needles plunged significantly in stressed seedlings compared to the control. For new needles, however, the difference between treatments did not become significant until more than three weeks later when the peat had dried still further to a WC of about 10%. Within the drought treatment, the needle age classes likewise began to differ significantly at 25% peat WC.

Based on the water availability distinctions in Study II, Fig. 3, the peat WC instigating a critical change in the level of  $F_v/F_m$  in the old needles of drought-stressed seedlings approximated with the permanent wilting point. By the time  $F_v/F_m$  began to descend markedly in new needles, however, the peat WC had already fallen well below this critical point. In effect, old Scots pine needles were more sensitive than new needles when oppressed by water shortage.

#### Drought-induced changes in polyamine concentrations

The free putrescine and spermidine concentrations in control seedlings were significantly higher overall than in drought-stressed ones, whereas the opposite was true concerning free spermine (Study II, Tables 1–2). However, the between treatment differences in putrescine and spermidine concentrations depended on time (Study II, Table 1). Prior to being moved into the heated green-



house proper (Aug. 27<sup>th</sup>) with soil WC at 25–30% (Study II, Fig. 4), the putrescine concentrations in roots and new needles of drought-stressed seedlings had risen considerably higher than their starting levels as well as in relation to the control (Study II, Fig. 6a, g). However, by the third time samples were taken (Sept. 30<sup>th</sup>) with soil WC at < 10%, putrescine concentrations had decreased in all sample types in the stress treatment with a dramatic decrease occurring particularly in new needles (Study II, Fig. 6a, d, g). Likewise, drought led to significantly lower spermidine concentrations than in the control on the last two sampling occasions when peat WC had already dropped below 10% (Study II, Fig. 6b, e, h). At this stage, the considerably lower spermidine concentration in fine roots of stressed seedlings accounted for the differences observed between treatments (Study II, Fig. 6b). Regarding spermine, the effect of drought was most plainly seen as a function of sample type as the concentration specifically in new needles rose significantly above the control level (Study II, Tables 1–2, Fig. 6c, f, i).

### Root and shoot characteristics

Except for the root-to-shoot ratio (Study II, Fig. 7a), drought stress significantly affected all other measured seedling morphological characteristics (Study II, Figs. 7b–c and 8a–d). Drought reduced the dry biomass and water content of both shoots and roots (Study II, Fig. 7b–c) as well as the number of fine root tips (Study II, Fig. 8a), while increasing the proportion of defunct tips (Study II, Fig. 8b). Severely reduced carbon allocation to root biomass in response to dry soil conditions was likewise reflected in the frequency of root-associated ectomycorrhizal fungi (Study II, Fig. 8c) as less than 40% of fine roots tips in stressed seedlings had sustained a symbiotic relationship. Furthermore, the quantity of living (i.e., not defunct) tips relative to dry root biomass was lower in drought-stressed than control seedlings (Study II, Fig. 8d).

### 3.2.2. Greenhouse experiment II: drought and waterlogging stress

#### Bulk density and water retention curve of peat substrate

Respective bulk densities were 0.07 and 0.10 g cm<sup>-3</sup> and total porosities 96 and 94% for the bottom and surface *Sphagnum* peats. Water retention at desorption (relative to volume at -0.3 kPa) is presented in Study III, Fig. 2. The permanent wilting point lay at approximately 10 and 12% soil water content for the bottom and surface peats, respectively. Conversely, the upper limit of available water equated with an 86% WC in the bottom peat and 84% WC in the more decomposed surface peat.

#### Soil water content and photochemical efficiency

The soil water conditions leading up to the onset of stress are shown in Study III, Fig. 3. Overall, both drought and waterlogging stress significantly reduced  $F_v/F_m$  of old needles relative to the control, but no such effect was evident for new needles (Study III, Table 1). In addition, new needles maintained significantly higher  $F_v/F_m$  than old needles in all treatments.

Unfavorable soil water conditions climaxed in a sustained decrease in  $F_v/F_m$ , but just when (and at what soil WC) this happened hinged on treatment and needle age (Study III, Table 1). The first indication of stress in old needles occurred in the wet treatment after the seedlings had spent 2 months in saturated soil conditions (Study III, Figs. 3 and 4). Thereafter (Aug. 5<sup>th</sup>),  $F_v/F_m$

declined steadily in the old needles of wet-stressed seedlings in respect to the control. Although a clear decrease in  $F_v/F_m$  in old needles of drought-stressed seedlings did not emerge until 2 weeks later (Aug. 19<sup>th</sup>) when soil WC had dropped to 14% (Study III, Fig. 3), the decline was more drastic than in the wet treatment. By experiment's end,  $F_v/F_m$  in old needles was markedly lower than in the control and wet treatments alike (Study III, Fig. 4). In the case of new needles, the only significant change observed in  $F_v/F_m$  befell the drought-stressed seedlings at the end of the experiment (Aug. 27<sup>th</sup>) when the soil had dried still further to 11% WC (Study III, Figs. 3 and 5).

Planting stress was generally apparent in old needles early on in the experiment (period 1.–15.6) as  $F_v/F_m$  fluctuated before finally stabilizing (Study III, Fig. 4). In new needles, the fluctuations occurring at the start (30.6–16.7) were probably due to needle immaturity (Study III, Fig. 5).

### Shoot and root traits

The consequences of the two types of stress—too little versus too much soil water—on shoot and root traits were dissimilar (Study III, Tables 2–4, Figs. 6–8). Relative to the control, drought significantly reduced: seedling height (Study III, Table 3); length of current-year terminal shoots, apical buds, and new needles (Study III, Fig. 6); thickness of current and previous-year terminal shoots (Study III, Fig. 6, Table 3); fresh mass of terminal bud groups and new needles (Study III, Fig. 6); root volume, root dry mass, and root hydraulic conductance rate ( $K_r$ ,  $\text{mg s}^{-1} \text{MPa}^{-1}$ ) (Study III, Figs. 7 and 8a). Waterlogged soil, on the other hand, did not markedly affect any of these traits compared to the control. The differences between treatments were insignificant regarding root surface area, area or volume-specific root hydraulic conductivity ( $L_{p(RA)}$ ,  $L_{p(RV)}$ ), length of fine roots and all roots combined (Study III, Tables 3–4, Figs. 7 and 8b).

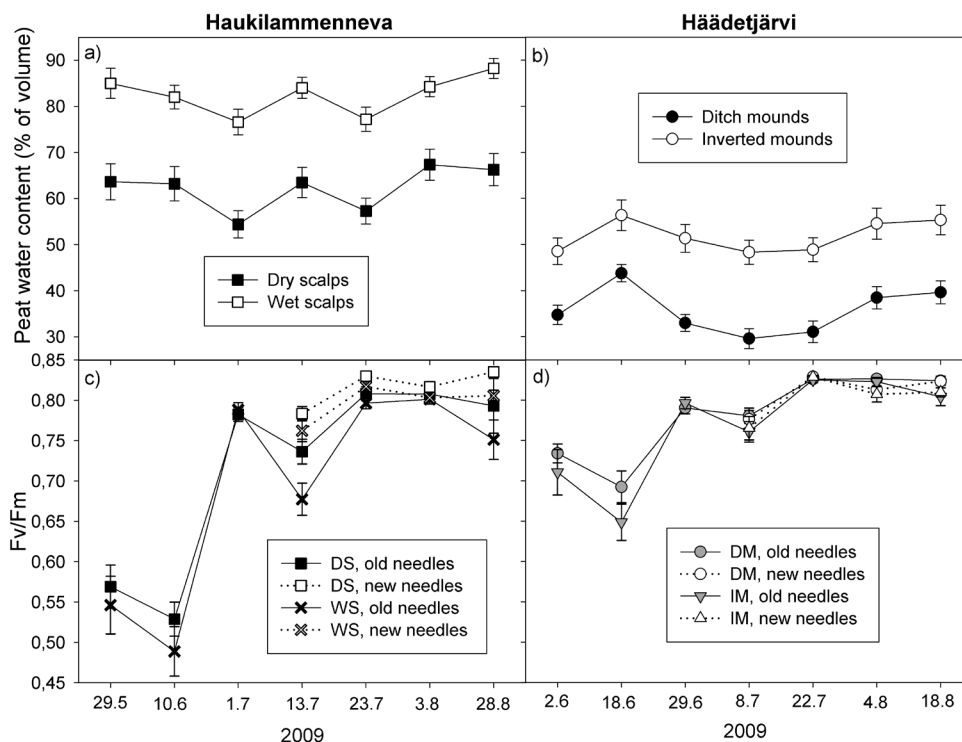
### Polyamine concentrations in response to drought and waterlogging stress

In line with the aforementioned results, the impact of drought was also most obvious as concerns free polyamine concentrations. Drought significantly increased free putrescine concentrations in new needles relative to the control (Study III, Table 5, Fig. 9a). Notably, the relationships between plant parts, i.e., sample types likewise varied according to treatment. Within the control, below-ground organs differed significantly from aboveground parts (new needles and shoots > roots); in comparison, wet stress leveled off between part differences in free putrescine such that none were significant, whereas drought stress emphasized these differences such that all were significant (new needles > shoots and roots, shoots > roots) (Study III, Fig. 9a–c). As for free spermine, the concentrations were distinctly greater in the drought-stressed than control seedlings for all sample types (Study III, Table 7, Fig. 9g–i). Conversely, the wet treatment did not significantly differ from the control for any of the free polyamines or sample types analyzed (Study III, Fig. 9a–i). Lastly, no differences were detected in free spermidine concentrations between treatments for any of the sample types (Study III, Table 6, Fig. 9d–f).

#### 3.2.3. Haukilammenneva and Häädetjärvi experimental sites: stress tolerance in field conditions

The respective soil moisture gradients within scalps (Haukilammenneva) and mounds (Häädetjärvi) are displayed in Fig. 6a–b and their mean WTLs in Table 1. In addition, their mean soil temperatures are provided in Table 2. Planting stress was evident the first two times of measurement in scalps and mounds alike as photochemical efficiency of old needles remained distinctly low before recovering to a normal level, i.e., 0.80 (Fig. 6c–d).





**Figure 6.** Photochemical efficiency ( $F_v/F_m$ ) of dark-adapted, previous-year (old) and current-year (new) Scots pine needles and corresponding soil water content at two forestry-drained, clearcut peatland sites. At each site, the same fifty seedlings growing in prepared microsites were measured every time. Each dot represents mean  $\pm$  SE. DS = dry scalps, WS = wet scalps, DM = ditch mounds, IM = inverted mounds.

Thereafter, photochemical efficiency ( $F_v/F_m$ ) in old as well as new needles generally followed the moisture gradient within scalps and mounds (Table 3, Fig. 6), i.e., the wetter the soil (WS > DS, IM > DM), the lower  $F_v/F_m$  (WS < DS, IM < DM). Scalps represented the scenario where too much soil water can induce inner turbulence, and indeed, seedlings in wet scalps indicated such stress as  $F_v/F_m$  was significantly reduced in both old and new needles compared to dry scalps (Tables 3–4). In fact, the most pronounced dives in  $F_v/F_m$  of old needles occurred when the soil WC in wet scalps had risen to approximately 85% (13.7 and 28.8) (Fig. 6c). Considering that the total pore volume in this type of peat (at midstage of decomposition) is about 90% (Päivänen 1973) and the minimum air content regarded necessary for so-called normal growth is 10% of volume, poor aeration apparently plagued wet scalps so much to cause photochemical efficiency to periodically drop in old needles. Mounds represented the scenario where too little soil water could initiate physiological unrest in seedlings, but no such stress ever materialized during the single summer of monitoring. Although photochemical efficiency tended to be higher in seedlings planted in ditch mounds than inverted mounds, the two did not significantly differ (Tables 3 and 5). In order to induce drought and a consequent effect on photochemical efficiency in the specified peat, the soil WC would have likely needed to decrease considerably below 30%, but here, the mean WC in ditch mounds was never less than that.

**Table 1.** Mean summertime water table level (with minimum and maximum) in prepared microsites at two forestry-drained, clearcut peatland sites. WTL is the depth below the soil surface expressed in cm.

Site	Treatment	WTL	Min–Max
Haukilammenneva	Dry scalps	34	31–38
	Wet scalps	22	18–27
Häädetjärvi	Ditch mounds	55	42–69
	Inverted mounds	39	26–48

**Table 2.** Mean summertime soil temperature ( $\pm$  SE) at 5 cm depth (T5) in prepared microsites at two forestry-drained, clearcut peatland sites. Temperature is expressed in °C.

Site	Treatment	Soil T5
Haukilammenneva	Dry scalps	13.74 $\pm$ 0.08
	Wet scalps	13.15 $\pm$ 0.08
Häädetjärvi	Ditch mounds	14.05 $\pm$ 0.10
	Inverted mounds	13.77 $\pm$ 0.10

**Table 3.** Mean photochemical efficiency of PSII,  $F_v/F_m$  ( $\pm$  SE), in planted Scots pine seedlings growing in prepared microsites at two forestry-drained, clearcut peatland sites.

Site	Treatment	Old needles	New needles
Haukilammenneva	Dry scalps	0.717 $\pm$ 0.011	0.817 $\pm$ 0.004
	Wet scalps	0.693 $\pm$ 0.012	0.797 $\pm$ 0.005
Häädetjärvi	Ditch mounds	0.782 $\pm$ 0.005	0.810 $\pm$ 0.004
	Inverted mounds	0.767 $\pm$ 0.008	0.803 $\pm$ 0.005

**Table 4.** Fixed effects of linear mixed model for  $F_v/F_m$  in scalps (Haukilammenneva).

Source	df	F	p
Time	3	23.610	0.000
Treatment	1	5.766	0.021
Needle age	1	18.464	0.000
Time*treatment	3	1.006	0.391
Time*needle age	3	3.447	0.018
Treatment*needle age	1	0.192	0.663
Time*treatment*needle age	3	0.450	0.717

While needle age had a significant effect on photochemical efficiency in seedlings planted in scalps, no such trend was evident in mounds (Table 5).  $F_v/F_m$  in old needles was always lower than in new ones within scalps (Table 3). Additionally, in wet scalps, old needles were clearly more sensitive to waterlogging stress than new ones (Table 3, Fig. 6c).

Despite the apparent impact of waterlogged soil on  $F_v/F_m$  in outplants growing in wet scalps, morphologically these seedlings were not affected as no differences between those in dry scalps were detected for any of the measured traits (Tables 6 and 8, Figs. 7b, d, f). In the two types of mounds, shoot water content was significantly higher in seedlings growing in ditch mounds, but no other contrasts were found (Tables 7–8, Figs. 7a, c, e).

**Table 5.** Fixed effects of linear mixed model for  $F_v/F_m$  in mounds (Häädetjärvi).

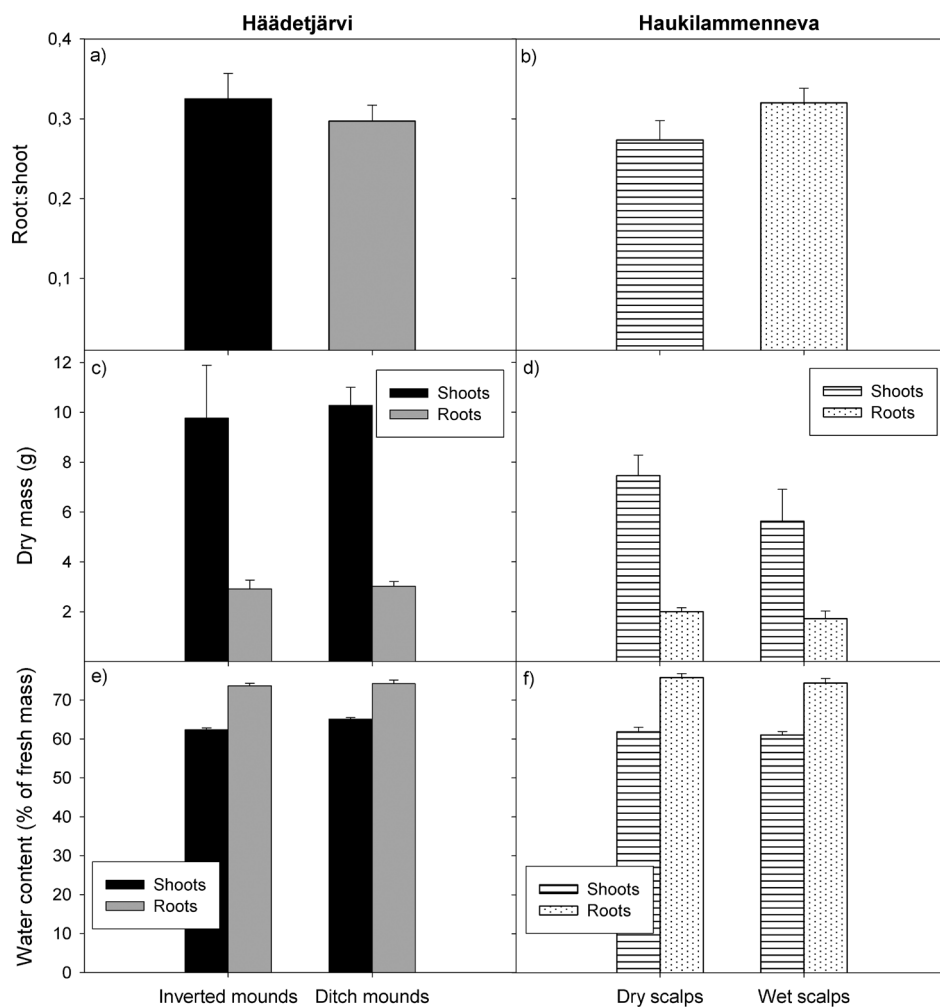
Source	df	F	p
Time	3	50.662	0.000
Treatment	1	2.801	0.101
Needle age	1	0.355	0.553
Time*treatment	3	1.219	0.304
Time*needle age	3	1.540	0.205
Treatment*needle age	1	0.191	0.663
Time*treatment*needle age	3	0.113	0.953

**Table 6.** Results of the one-way ANOVA for testing the treatment effect on various shoot and root characteristics of seedlings in scalps (Haukilammenneva).

Trait	df	F	p
Seedling height	1	0.119	0.732
Length of current-year terminal shoot	1	0.074	0.787
Root:shoot	1	2.387	0.161
Shoot dry mass	1	1.128	0.319
Root dry mass	1	0.482	0.507
Shoot water content	1	0.297	0.600
Root water content	1	0.686	0.432

**Table 7.** Results of the one-way ANOVA for testing the treatment effect on various shoot and root characteristics of seedlings in mounds (Häädetjärvi).

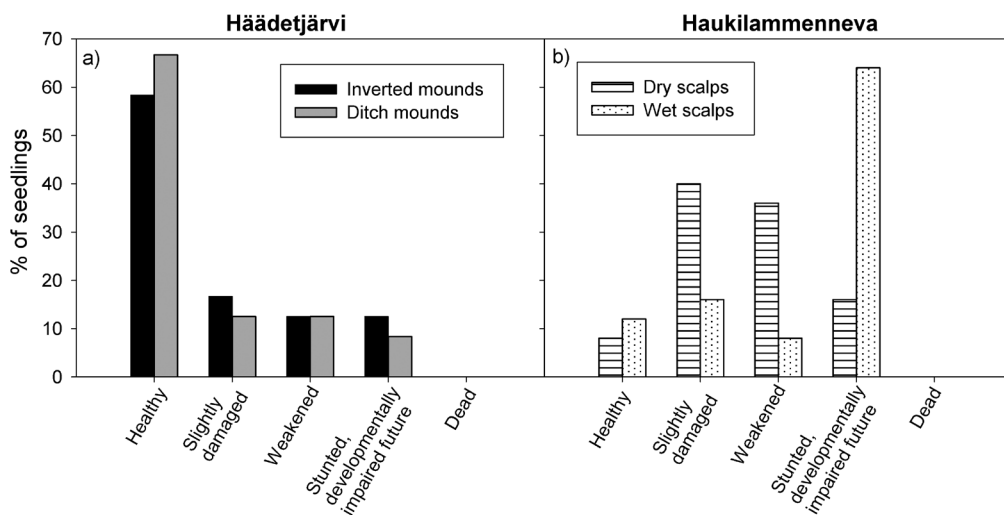
Trait	df	F	p
Seedling height	1	0.565	0.456
Length of current-year terminal shoot	1	0.484	0.490
Root:shoot	1	0.559	0.476
Shoot dry mass	1	0.052	0.826
Root dry mass	1	0.064	0.806
Shoot water content	1	19.827	0.002
Root water content	1	0.190	0.675



**Figure 7.** Carbon allocation and water content of two-year-old, planted Scots pine seedlings after their first summer growing in prepared microsites at two forestry-drained, clearcut peatland sites. Five seedlings per microsite type (20 total) were examined.

**Table 8.** Length of current-year terminal leader shoot and height (mean  $\pm$  SE in cm) of two-year-old Scots pine seedlings at the end of the first summer following outplanting in prepared microsites at two forestry-drained, clearcut peatland sites. One-hundred seedlings total were surveyed.

Site	Treatment	Terminal shoot growth	Seedling height
Haukilammenneva	Dry scalps	12.62 $\pm$ 1.03	34.15 $\pm$ 1.27
	Wet scalps	12.29 $\pm$ 0.70	33.51 $\pm$ 1.32
Häädetjärvi	Ditch mounds	16.28 $\pm$ 0.89	33.10 $\pm$ 1.27
	Inverted mounds	15.47 $\pm$ 0.76	34.32 $\pm$ 1.02



**Figure 8.** Vitality of two-year-old Scots pine seedlings in prepared microsites after the first summer following planting at two forestry-drained, clearcut peatland sites. One-hundred seedlings total were surveyed.

Noticeably, the seedlings in both dry and wet scalps extensively suffered bud and needle damage due to browsing by grouse at the Haukilammenneva site. Those individuals, which had avoided this fate, were an absolute minority. In addition, old needles in about half the seedlings in wet as well as dry scalps had commonly yellowed and dropped off. Conversely, seedlings in mounds at the Häädetjärvi site had been for the most part left to grow in peace. However, rather extensive yellowing of old needles was also observed in 40% of the seedlings planted in the low inverted mounds.

As for seedling vitality, 75–80% of the seedlings in both types of mounds were either *healthy* or at worst just *slightly damaged* (Fig. 8a). In scalps, on the other hand, very few seedlings were in a healthy state, but those in wet scalps were especially battered as 65% were deemed *stunted with a developmentally impaired future* (Fig. 8b). Around 80% of the seedlings in dry scalps were *slightly damaged* or *weakened*. However, on a positive note, none of the seedlings had deceased at either site.

### 3.3. Influence of soil preparation on soil environment: WTL, soil temperature, C:N

Soil preparation led to a wide range of soil moisture conditions due to the shift in WTL relative to the soil surface. With respect to control (unprepared) microsites, the distance to the WTL increased in mounds but decreased considerably in scalps (Study I, Table 1, Fig. 3). The latter was also true for pits. In fact, the WTL commonly fluctuated above and below zero in these two types of depressions throughout the study period (Study I, Fig. 3; Study IV, Fig. 5, Table 2). During heavy rainfall (or snowmelt) as in the 2008 growing season (Study I, Fig. 2; Study IV, Fig. 2), runoff typically drained into scalps and pits. This accumulation of supersurface water on the exposed peat lingered for days on end even during drier periods. Furthermore, when scalps and pits were already underwater, they often received supplemental runoff. Due to the dynamic

nature of these water relations, the water table readings measured from the tubes next to scalps, in particular, normally did not correspond to the presence of supersurface water (i.e., indicating only that the WTL was near but still below the soil surface).

The differing hydrology of the Northend and Southend blocks was evident for nearly all microsite types (Study IV, Table 2, Figs. 4–5). Generally, the WTL was about 10 cm higher in the Northend than Southend. Also, the WTL reached its maximum depths namely in the Southend for all prepared and unprepared microsite types (Study IV, Figs. 4–5). Coincidentally or not, the mean WTL was higher in the unprepared microsities within the mounded plots than those in the control plots for both blocks (Study IV, Table 2). In addition, pits in the Northend mounded plot were nearly always inundated, sometimes with as much as 20 cm of water (Study IV, Fig. 5b). Furthermore, while the mound top—where seedlings are planted—was situated well above the WTL in the Northend, the same could not be said for the mound bottom—where “new” carbon is situated—as the WTL commonly rose to a distance of as little as 5 cm from it (Study IV, Fig. 4a). Thus, these factors combined to make the mounded plot in the Northend soggy than all the rest. Ironically, within mounded plots, the creation of drier microsities (mounds) also resulted in wetter prepared microsities (pits) as a by-product as well as wetter unprepared microsities relative to the control treatment plots.

Only slight differences in soil temperature (5 and 30 cm depths) were observed after soil preparation (Study I, Table I; Study IV, Table 2). On the whole, elevated WTLs combined with plentiful rainfall leading to high moisture levels, which effectively drowned out any noticeable warming effect of soil preparation. Thus, in this research, soil preparation influenced peat moisture more than temperature conditions throughout.

Repositioning of the peat substrate through soil preparation had consequences for nutrient reserves. However, the analysis of C and N concentrations and C:N in planting spots—mounds, scalps, control microsities—revealed somewhat unexpected results. When considering the 0–20 cm layer overall, namely mounds had the highest C and lowest N concentrations as well as the highest C:N (Study I, Tables 2–3, Fig. 5). Remarkably, the N concentration in mounds increased from top (0–10 cm) to bottom (10–20 cm), i.e., from the most to least decomposed portion (Study I, Table 3). In the control microsities, the trend was just the opposite as the deeper soil samples (10–20 cm) were richer in N than the shallower ones (0–10 cm) (Study I, Table 3). Scalps typically represented the middle ground between mounds and control microsities (Study I, Table 3, Fig. 5). Generally, N concentrations were greater and C:N lower in the Northend than Southend planting spots (Study I, Table 3, Fig. 5). In the Northend, N concentrations were highest and C:N lowest in control microsities, but in the Southend such was the case in scalps.

### 3.4. Impacts of soil preparation on peat decomposition ( $SR_p$ ), $CH_4$ and $N_2O$ fluxes

#### 3.4.1. From instantaneous $CO_2$ fluxes of microsities to annual $CO_2$ fluxes by treatment

In respect to the control microsities,  $CO_2$  emission resulting from the microbial breakdown of organic matter did not markedly differ in mounds overall, but instead emissions from scalps and pits were significantly reduced (Study IV, Tables 4–6, Fig. 3a). However, these responses were controlled by the WTL variations occurring over time (microsite type\*time interaction, Study IV, Table 5). Whenever the WTL in mounds (Study IV, Table 2, Fig. 4a), especially Northend ones, rose closer to their bottom section during the growing season,  $CO_2$  emissions from mounds were

in fact significantly lower than from control microsites. In scalps and pits, a dynamic relationship between the  $\text{CO}_2$  flux and WTL was also prominent (Study IV, Fig. 6). The flux was lowest when the WTL was at zero (soil surface level), but it increased not only as the microsite dried (WTL dropped) but also when the WTL rose above the surface of the microsite. Notably, soil preparation also intensified instantaneous  $\text{CO}_2$  emission from the unprepared microsites within the mounding and scalping treatment plots relative to the control ones (Study IV, Tables 4 and 7–8, Fig. 3a).

Although differences in instantaneous  $\text{CO}_2$  effluxes were apparent between microsite types (Study IV, Figs. 3a and 8–9, Tables 4–8), simulated annual  $\text{CO}_2$  emission rates were strikingly similar between treatments (Study IV, Fig. 10a), i.e., when the surface area-based distribution of microsite types in the corresponding treatment plots were taken into consideration. Thus, relative to the control, soil preparation had little or no effect on annual  $SR_p$  on either of these clearcut, nutrient-poor drained peatland blocks.

### 3.4.2. From instantaneous $\text{CH}_4$ fluxes of microsites to annual $\text{CH}_4$ fluxes by treatment

Compared to control microsites,  $\text{CH}_4$  emissions decreased significantly from mounds overall (i.e.,  $\text{CH}_4$  was oxidized) and this trend was equally apparent in both blocks (Study IV, Tables 4–6, Fig. 3b). Scalps and pits, however, did not markedly differ from the control overall. Importantly, the differing hydrology of the blocks could be plainly seen in the  $\text{CH}_4$  flux behavior of control microsites and pits; as opposed to the Southend, these microsite types in the Northend were clear sources of  $\text{CH}_4$  (Study IV, Fig. 3b, Table 4). Thus, the block effect was significant (Study IV, Table 5).

Likewise, when contrasting the unprepared microsites of different treatments, the role of block was prominent (Study IV, Table 7). This was due to the contrary  $\text{CH}_4$  flux responses of the unprepared microsites within the control and mounding treatments; while they were obvious sources of  $\text{CH}_4$  in the Northend, they typically consumed  $\text{CH}_4$  in the corresponding treatments plots of the Southend (Study IV, Table 4, Fig. 3b). Namely, the unprepared microsites in the Northend mounded plot, which released the most  $\text{CH}_4$  (Study IV, Fig. 3b), had the greatest cover of cottongrass (Study IV, Table 9) in addition to the highest mean WTL (Study IV, Table 2).

Notably, unusual interplay between  $\text{CH}_4$  emission and the WTL was observed within scalps. Whenever the WTL dropped in scalps,  $\text{CH}_4$  emission increased (Study IV, Fig. 7). When the WTL once again rose,  $\text{CH}_4$  emission from scalps correspondingly decreased.

With regard to simulated, annual treatment level  $\text{CH}_4$  flux rates, the mounding treatment—inclusive of mounds, pits, and unprepared microsites—clearly stimulated  $\text{CH}_4$  emission from soil relative to the other two treatments in the soggy conditions of the Northend (Study IV, Fig. 10b). All three treatments there, however, led to annual  $\text{CH}_4$  emission rates greater than those reported by Ojanen et al. (2010) for this site type (see Section 2.1.). On the contrary, in the Southend, where drainage was sufficient, the unprepared and mounding treatments led to  $\text{CH}_4$  oxidation of similar magnitude as that in Ojanen et al. (2010). The similarities in WTL and cottongrass coverage (Study IV, Tables 2 and 9) between blocks in the scalping treatment were likewise reflected in the amount of  $\text{CH}_4$  emitted annually (Study IV, Fig. 10b).

### 3.4.3. From instantaneous $\text{N}_2\text{O}$ fluxes of microsites to annual $\text{N}_2\text{O}$ fluxes by treatment

Overall mounds, which were the greatest sources of  $\text{N}_2\text{O}$  on average, stood out significantly from control microsites in addition to scalps and pits (Study IV, Tables 4–6, Fig. 3c). These latter three mentioned, however, did not differ in their instantaneous  $\text{N}_2\text{O}$  flux rates (Study IV, Table 6).

Furthermore, similar to the CO<sub>2</sub> results, both soil preparation methods also increased N<sub>2</sub>O fluxes from the unprepared microsites within prepared plots compared to the control in the Northend as well as the Southend (Study IV, Table 4, Fig. 3c). Overall, however, only those in the scalping treatment diverged significantly from the control (Study IV, Tables 7–8, Fig. 3c).

When shifting the focus from the instantaneous fluxes of individual microsite types to simulated annual fluxes of entire treatments, soil preparation accelerated the annual emission of N<sub>2</sub>O relative to the control treatment in both blocks (Study IV, Fig. 10c). These annual N<sub>2</sub>O emission rates were low but nonetheless typical for nutrient-poor drained peatlands (Ojanen et al. 2010). Strangely, the soil preparation method causing the least disturbance, scalping, resulted in the greatest annual emission of N<sub>2</sub>O.

#### *3.4.4. Global warming potential of soil preparation treatments*

While differences in CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O fluxes were apparent between microsite types as well as entire treatments, the combined impact—all gases considered in terms of CO<sub>2</sub> equivalents over a 100-year time span (100-year GWP values)—of the mounding and scalping treatments was null (Study IV, Fig. 11). Oddly, the block factor—differing hydrology—also lost importance. Hence, the global warming potential (100 years) of this clearcut nutrient-poor drained peatland was not altered by soil preparation in the short term.



## 4. DISCUSSION

### 4.1. Regeneration success

On thick-peated soils, provision of well-aerated growing spots, i.e., in the form of mounds for Scots pine outplants was the decisive factor dictating regeneration success (Study I). Any other possible benefits related to soil preparation, such as reduced competition with other plants, are of secondary importance if surplus water cannot be expelled as was observed in scalps. However, neither low nor high intensity mechanical soil preparation actually increased soil temperatures or the rate of organic matter decomposition. Furthermore, no favorable impact of soil preparation on C:N or N concentrations was discerned either. While factors other than WTL were of negligible importance here in the short-term regeneration success of Scots pine seedlings, these may nonetheless become influential in the long run as their shoot and root systems expand and nutritional demands increase. In addition, the unexpected finding that both methods of soil preparation heightened decomposition namely in the intact unprepared microsites remaining in prepared plots could have serious implications for practical forestry. It may lead to greater nutrient availability for plants competing with Scots pine seedlings, which would ultimately expedite the spread of other vegetation and less valuable tree species (e.g., downy birch) on peatland forest regeneration sites (Study IV).

Consistent with Kaunisto and Päivänen (1985) and Sutton (1993), the higher position of seedlings growing in mounds provided them with favorable moisture conditions thus improving survival. After three growing seasons in the field, however, the growth and vitality of seedlings in mounds and unprepared spots were similar. This is contrary to previous findings, albeit with slightly older Scots pine outplants, that mounding accelerates seedling growth compared to leaving soil unprepared on drained clearcut peatlands (Mannerkoski 1975, Kaunisto 1984). On the other hand, the equivalent growth observed in mounds and unprepared spots in Study I conforms to the results of Hendrick (1984) with lodgepole pine, and Takyi and Hillman (2000) with tamarack and black spruce.

Foremost, the survival of Scots pine seedlings in unprepared planting spots was compromised by the European pine weevil (Study I, Table 5) and planting spot elevation. Although the benefits of soil preparation in reducing pine weevil damage to tree seedlings have been recognized namely on mineral soils (Hånell 1993, von Sydow 1997, Heiskanen and Viiri 2005), these results suggest that soil preparation by mounding may reduce the risk of damage to planted seedlings also on (wet) organic soil.

The elevation of unprepared planting spots (Roy et al. 1999) together with surrounding transpiring vegetation (e.g., Verry 1988) likely determined whether WTL became a survival inhibiting factor or not in the control treatment. Particularly the higher than average rainfall and consequently high WTL during the 2008 summer (Study I, Figs. 2–3) would have hit seedlings planted in low-lying lawn surfaces of the Northend control plot hardest. Careful consideration of microrelief, peat characteristics, species, and local climate prior to planting could potentially improve the survival rate in unprepared peatland forest regeneration sites (Rothwell et al. 1993, Roy et al. 1999). On this relatively nutrient-poor forestry-drained site, competition with field vegetation at this stage was limited and pine seedlings planted in control plots primarily competed with mosses. Hence, competition was not yet a crucial determinant of outplant survival.

Excess moisture in scalps, particularly arising during the second summer after outplanting (2008), proved fatal to planted Scots pine seedlings. Dispersion and/or percolation of surplus

water was limited and slow compared to mounds and unprepared spots. Even in the relatively drier 2009 growing season, WTL fluctuations above and below ground level were still evident in both Northend and Southend scalps, which is indicative of their hydrological sensitivity. If the range of potential maintenance drainage procedures is restricted by water quality concerns associated with nearby watercourses, as was the case at the Joenvarsisuo site (Studies I and IV), then the credibility of the scalping method inevitably suffers in association with clearcutting on thick-peated soil. Higher than average rainfall only compounds the potential for regenerative failure in scalps. Clearly, even leaving the soil unprepared would be a smarter option in such circumstances.

## 4.2. Seedling tolerance to drought and waterlogging stress in genuine peat soil over one growing season

### 4.2.1. In controlled conditions

Scots pine seedlings demonstrated high tolerance to adverse soil water conditions—too little or too much water—occurring in genuine peat soil *over one growing season* in a controlled environment. Namely, drought did not kill seedlings until all available water in the peat had vanished (Study II). Moreover, none of the seedlings perished in response to waterlogged peat soil during the first post-planting growing season (Study III). Aside from mortality, however, the impacts of the two stressors differed considerably with drought leading to more immediate (i.e., already apparent during first growing season) and severe changes in seedling morphology, physiology, and metabolism.

As part of their tolerance strategy, the maximum potential photochemical efficiency of PSII expressed as  $F_v/F_m$  in Scots pine seedlings was not easily altered by extreme drought or waterlogging. Based on our results, water-associated stress in Scots pine seedlings has to be severe before needle photochemical efficiency is impacted. Similarly, Otronen and Rosenlund (2001) found no impact on  $F_v/F_m$  ratios of current-year needles in Scots pine seedlings grown at five different soil moisture levels ranging from 10–80%. They did not, however, monitor  $F_v/F_m$  of previous-year needles. On the same line, Binder et al. (1996) observed a drop in  $F_v/F_m$  only after severe drought in jack pine (*Pinus banksiana* L.), while no indication of water stress in the  $F_v/F_m$  ratio was evident in Masson pine (*Pinus massoniana* L.) seedlings subjected to wet, medium, and dry soil moisture treatments (Fang-yuan and Guy 2004).

Here, the lower and upper limits of available water (i.e., permanent wilting point and 10% soil air content, respectively) in both the *Carex* and *Sphagnum* peats had to be reached before inducing a sustained change in photochemical efficiency. Furthermore, the tendency of old needles to give way first, i.e., incur reduced photochemical efficiency likely as a means of protecting new needles, was evident in the response to both stress treatments. This response conforms with the known tactic of shifting growth resources within Scots pine, e.g., nutrient retranslocation from old needles to developing new needles and elongating shoots (Fisher and Höll 1991, Helmisaari 1992). Under water stress, new needles were in effect prioritized, which is in accordance with most net photosynthesis being due to current-year needles in Scots pine in the latter half of the growing season (Ericsson 1979, Gezelius and Hallen 1980, Vapaavuori et al. 1995, Iivonen et al. 2001). Such an “investment” strategy and maintenance of high photochemical efficiency in current-year needles would likely aid post-stress recovery in the event that soil water availability or soil aeration would once again improve.

On a cautionary note, it should be kept in mind that  $F_v/F_m$  measured from dark-adapted needles is only a measure of *maximum potential* photochemical efficiency (i.e., if all capable reaction centers of PSII were open), not effective, i.e., *achieved* yield of PSII. The latter, which is measured under steady-state photosynthetic lighting conditions, indicates just how much energy is actually used in photochemistry by PSII, and thus recognizes heat dissipation (NPQ) as a means of dealing with water stress especially in the early and middle stages (Genty 1989, Maxwell and Johnson 2000, Rascher et al. 2000, Mohammed et al. 2003). Hence, even though Scots pine is known to close stomata early on to limit water stress (Picon-Cochard et al. 2006), which consequently lowers transpiration, respiration, as well as net carbon assimilation (Panek 2004, Zweifel et al. 2005, 2007, Breda et al. 2006, Matyssek et al. 2006, Sterck et al. 2008), lowered stomatal conductance does not necessarily affect maximum potential photochemical efficiency. In this respect, the  $F_v/F_m$  parameter was not a particularly sensitive indicator of physiological turmoil in response to drought or wet stress as demonstrated here. On the other hand, as Bukhov and Carpentier (2004) and Bigras (2005) have pointed out, the required minimum water content to ensure functioning of the photosynthetic apparatus depends on the plant species. In any case, these results show that the integrity of PSII in Scots pine is not readily compromised.

Curtailed shoot and root growth is a commonly observed response to drought amongst pine seedlings (Kaufmann 1968, Rikala and Puttonen 1988, Torreano and Morris 1998, Otronen and Rosenlund 2001, Sword Sayer et al. 2005) and the findings of Studies II and III also confirm this. Furthermore, inadequate bud formation in drought-stressed seedlings (Study III) would have a carry-over effect into the next growing season. In examining the growth response to drought, it is important to consider the timing of the stress in relation to shoot and root phenology. A few studies have shown that root growth is depressed during shoot and needle elongation in young seedlings of Scots pine (Mattsson 1986, Iivonen et al. 2001). Since growing shoots are strong consumers of assimilates (Lyr and Hoffmann 1967, Iivonen et al. 2001), root growth tends to be most intense towards the end of the growing season when shoot growth is nearly complete (Iivonen et al. 2001). In Studies II and III, the growth of shoots and new needles, in particular, was still in progress when soil water became a limiting factor, which then climaxed in shorter current-year needles and shoots and lower shoot dry mass in the drought treatment. Furthermore, during their “window of growth”, there was simply not enough water available for roots to grow and this was reflected as reduced root volume and dry mass in drought-stressed seedlings. In drying soil, Kaufmann (1968) observed that a soil water potential of  $-0.6$  to  $-0.7$  MPa ( $-600$  to  $-700$  kPa) encumbered root growth in Scots pine seedlings to a rate of only 25% of that at field capacity, and this equates well with the present results.

In addition to reducing carbon allocation to roots, drought suppressed fractional colonization of ectomycorrhizal fungi (Study II). Accordingly, decreased belowground carbon allocation to the root system and fungal association under dry conditions may be linked to decreased microbial activity in the peat soil. If we consider that mounding only had a modest effect on peat decomposition probably in part due to the disruption of the microbial community (Studies I and IV), then it seems reasonable that drought could further this trend.

While immediate growth losses were substantial in Scots pine seedlings due to drought, such was not the case in response to the wet treatment in controlled conditions. Although the seedlings spent three months in waterlogged peat during the growing season, i.e., when most vulnerable, neither shoot nor root growth was affected. Such resilience to saturated soil conditions is not, however, unheard of. For instance, Mukassabi et al. (2012) reported high Scots pine seedling survival rates even after 25 dormancy-free months in waterlogged soil. The described nonresponsiveness of shoots and roots to excess moisture has also been demonstrated earlier with

Scots pine (Armstrong and Read 1972, Zaerr 1983, Otronen and Rosenlund 2001, Mukassabi et al. 2012) and lodgepole pine (Armstrong and Read 1972, Boggie and Miller 1976, Wolken et al. 2011). Several theories have been proposed to explain the tolerance of Scots pine to flooding. Armstrong and Read (1972) suggested an internal oxygen diffusion pathway from shoot to root in anaerobic soil conditions. When placed in anaerobic soil, substantial oxygen diffusion from the roots of Scots pine seedlings was observed, which could be interpreted as successful adaptation to wet soil. Another potential mechanism is the formation of hypertrophied lenticels on submerged stems and roots, which has been noted in many pine species (Topa and MacLeod 1986a, 1986b, Kozłowski 1997) including Scots pine (Hahn et al. 1920, Aronen and Häggman 1994). The development of aerenchymatic tissue in the stems and roots of several pine species has also been identified as an effective strategy in dealing with waterlogged soil (Philipson and Coutts 1980, Topa and MacLeod 1986b, Wolken et al. 2011). Increased stem diameter growth in flooded Aleppo pine (*Pinus halepensis* Miller) seedlings has been attributed to bark thickening caused by parenchyma cell proliferation in the phloem (Yamamoto et al. 1987). It is worth noting, that the mean diameters of both the previous-year and current-year terminal shoots in the wet treatment were also larger here—though not significantly—than in the control (Study III, Table 3, Fig. 6b). In any case, each of the aforementioned adaptation strategies either alone or in combination would serve to facilitate gas exchange, dispersion of ethylene, and aeration of submerged roots at least in the short term. Also, the leeway for achieving normal root growth in waterlogged soil may indeed be narrow as Mukassabi et al. (2012) pointed out. Notably, Scots pine seedling roots were considerably shorter and lower in dry mass namely when the water table was 0–4 cm below the soil surface rather than 6.6 cm. In the latter case, seedling roots resembled those in the control treatment, which corresponds well with the findings of Study III. Moreover, although Study III attempted to emulate surplus moisture stress commonly encountered in field conditions, i.e., in scalps, one drawback of the experimental design is that it does not consider the input of water from above through precipitation since the seedlings were never watered from the top. Additionally, the high water level was steadily maintained. In the field, water tables in peat fluctuate considerably and interact with precipitation (Study I), thus having a more dynamic impact on seedling welfare than in a controlled, stable greenhouse environment. As Studies I and IV revealed, soil aeration in scalps was compromised due to a high WTL and standing water. Though precipitation and consequent runoff draining into scalps during rainy periods provided an input of oxygen, the runoff also contained readily decomposable organic carbon, the decay of which would have consumed oxygen in scalps (Section 4.3.1.).

Root hydraulic conductance ( $K_r$ ) and conductivity ( $L_p$ ) indicate the water uptake capability of roots. Roots with high hydraulic conductance are less resistant (i.e., more permeable) to water flow than those with low hydraulic conductance (Aroca et al. 2012). Typically, root resistance to water flow increases in response to stress—e.g., drought or poor root aeration due to waterlogged soil—consequently leading to reduced root hydraulic conductance (e.g., loblolly pine, Lee et al. 1990; tamarack and black spruce (*Picea mariana* (Mill.) B.S.P.), Islam et al. 2003, 2004; southern pines, Sword Sayer et al. 2005). Increased root lignification and suberization have been implicated in decreased root permeability and hydraulic conductance (Sands et al. 1982, North and Nobel 1991, Lo Gullo et al. 1998, Trifilo et al. 2004).

In Study III (Fig. 8a), only drought lowered  $K_r$  of two-year-old Scots pine seedlings. However, when  $K_r$  was scaled by root volume or surface area, no significant differences in root conductivity ( $L_p$ ) were observed between treatments (Study III, Fig. 8b, Tables 3–4). Decreased  $K_r$  was accompanied by corresponding reductions in root dry mass, surface area, and volume in drought-stressed seedlings. By the time root conductance and conductivity were measured, their roots

were obviously under considerable stress and some of them had likely already become damaged consequently losing their resistance mechanism. A loss in resistance due to root tissue damage and cell death would entail increased movement of water into roots and thus reflect as increased  $L_p$  (or equal to other treatments). As Kramer and Boyer (1995) noted, the movement of water into roots is decreased by stress treatments but conversely increased by killing the roots. Similar conclusions as ours have been previously reached by at least Apostol and Zwiazek (2003) for jack pine although not with drought stress. A combination of oxygen-depleted and salty conditions reduced root dry mass and  $K_r$  but increased  $L_p$  (scaled by root dry mass) in their seedlings (Apostol and Zwiazek 2003).

Considerable variability in the effects of waterlogging stress on root hydraulic conductance, conductivity, and seedling vitality and growth, in general, is evident within the Pinaceae family (Kozłowski 1997). Notably,  $K_r$  and  $L_p$  of two-year-old Scots pine seedlings were not affected by waterlogged soil in Study III. In the study of Apostol and Zwiazek's (2003) mentioned previously, purely hypoxic conditions however reduced root dry mass and both  $K_r$  and  $L_p$  in half-year-old jack pine. Our findings agree with Reece and Riha (1991) but contrast with those of Islam et al. (2003, 2004) for tamarack, a typical tree species on boreal peatlands in North America. Seedling age (and thus degree of tolerance) may account for some of this incongruence, as Reece and Riha (1991) used two-year-old while Islam et al. (2003, 2004) 6- and 18-month-old seedlings. Even within the latter mentioned studies  $K_r$  ranged from 5–8  $\text{mg s}^{-1} \text{MPa}^{-1}$  in the flooded 18-month-old tamarack seedlings but only from 2.5–4.5 in the half-year-old ones. Unlike in Study III, these seedlings were submerged to the root collar level.

When considering the metabolic response of Scots pine seedlings to water-associated stress, the impact of drought was also more pronounced than the wet treatment. In Study III, drought increased free putrescine levels in new needles as well as those of spermine in new needles, shoots, and fine roots relative to the control treatment, whereas the wet treatment did not significantly differ from the control for any of the free polyamines or sample types analyzed. These polyamine changes in drought-stricken needles of two-year-old Scots pine seedlings (Study III) were in line with Study II with one-year-old seedlings, in which however, putrescine concentrations collapsed in the new needles at the end of the experiment under extreme drought when soil water was no longer available (i.e., well below the permanent wilting point of the peat in question). This was suggestive of severe limitation in polyamine synthesis in the photosynthesizing tissues under extreme drought and was also accompanied by decreased  $F_v/F_m$  in new needles (Study II, Figs. 4 and 5).

Contrary to the observations from Study II, spermidine concentrations were not affected by the drought treatment in Study III. However, in Study II the higher spermidine level in the roots of sufficiently watered one-year-old seedlings was attributed to the significantly higher number of mycorrhizal root tips, which are known to increase spermidine concentrations in Scots pine seedlings (Niemi et al. 2006, Sarjala et al. 2010). In Study III mycorrhizal root tips were not counted, but no significant effect of drought stress was found on the length of fine roots at the end of the experiment, which may partly explain the lack of an effect on the spermidine level in the roots. Furthermore, seedlings were older, thus perhaps more resistant, and the drought inflicted was not quite as severe as in Study II as evidenced by the higher photochemical efficiency of drought-stressed old and new needles in Study III compared to Study II. The role of both spermidine and spermine has been suggested to be connected to regulation of senescence (Moschou et al. 2012) and furthermore, spermine has been shown to protect leaves from decay of photosystem complexes (Serafini-Fracassini et al. 2010). Hence, the higher spermine levels in the new needles of drought-stressed Scots pine seedlings in Studies II and III may have protected



the photosynthetic machinery so as to sustain higher  $F_v/F_m$  in the new needles until the bitter end. Interestingly, drought stress also amplified the difference in polyamine concentrations between the above and belowground plant parts mostly by elevating concentrations in the needles (Study III). This suggests that the aboveground parts of the seedlings were preferred to maintain functionality while roots were more susceptible to senescence under extreme drought stress. All in all, similarly to the findings of Tang et al. (2007) with transgenic pine, higher polyamine levels in Scots pine seedlings appeared to be associated with increased drought tolerance.

#### 4.2.2. Field observations in respect to those made in controlled environment

The seedlings planted in scalps at the Haukilammenneva site and in mounds at the Häädetjärvi site originated from the same batch of containerized seedlings used in Study III. Thus, it is worthwhile to illustrate just how strongly the experimental environment—a controlled versus field setting—influences seedling tolerance to stress. Compared to the greenhouse setting, in the field: 1) new needles emerged later and were thus not measurable until two weeks later; 2) planting stress was more severe at the start as evidenced by lower  $F_v/F_m$  in old needles; 3) fluctuations in photochemical efficiency were greater throughout and mean levels regularly lower; 4) seedlings were shorter in height and current-year terminal shoot length; 5) water input from above as rain, laterally as runoff, as well as from below (WTL) created a dynamic love-hate relationship between peat soil and seedling; 6) an unforeseeable risk of seedlings being molested by animals existed; and, 7) achieved vitality was the difference between benevolent and malevolent environmental factors with multiple stressors often occurring simultaneously. These general observations serve to highlight what we are dealing with in practice in peatland forest regeneration areas and remind us why controlled (greenhouse) experiments, no matter how well planned or implemented, are just that. Nonetheless, in addition to differences, similar trends were also visible in both settings.

Perhaps the most intriguing finding of the field experiment pertaining to mounds and scalps was that increasing soil moisture seemingly reduced photochemical efficiency, i.e., the wetter the soil, the lower  $F_v/F_m$ . This was especially true within scalps, as seedlings growing in wet scalps were plainly bogged down by periodically poor aeration (air content < 10%), which was reflected in extreme  $F_v/F_m$  lows in old needles (Fig. 6). On the contrary, the perturbations in  $F_v/F_m$  in the wet-stressed seedlings in the greenhouse experiment were essentially cosmetic (Study III, Fig. 4). This would seem to suggest better soil aeration due to a nonfluctuating WTL and the exclusion of the precipitation factor (with associated lateral water flow via runoff) in the greenhouse experiment.

On the other hand, seedlings in scalps were besieged by not just one individual stressor (waterlogged soil), but rather a series of stressors starting with planting stress which graduated to browsing and waterlogging stress along the way. Their impacts are not easily separated from one another and likely one may intensify the effect of the other. Hence, the malevolent factors outweighed the benevolent ones, which led to diminished seedling vitality in scalps (Fig. 8). The rather low photochemical efficiency of old needles even in dry scalps could indeed be a consequence of extensive browsing at the Haukilammenneva site; for instance, seedlings in mounds at the Häädetjärvi site were primarily left unmolested and  $F_v/F_m$  of old needles was noticeably higher. The soil water content ranged between 30–40% in ditch mounds and 50–60% in inverted mounds, which based on the drought stress results of the greenhouse experiments (Studies II and III) was sufficient to maintain normal  $F_v/F_m$  in Scots pine seedlings, i.e., drought-related stress was not apparent in mounds.

Notably, the differing moisture levels within *comparable* microsites—dry vs. wet scalps and

ditch vs. inverted mounds—only marginally influenced seedling morphological traits (e.g., growth) and vitality although a physiological consequence (i.e.,  $F_v/F_m$ ) was evident within scalps. Thus, it would appear that the type of scalp (wet or dry based on median WTL) or mounding technique used (ditch or inverted) is irrelevant at least when considering the well-being of outplanted seedlings after the first growing season. The 2009 summer when these field seedlings were monitored in the realm of Parkano was also an ordinary summer by Fennoscandian standards, being neither too wet nor hot, and in this sense these field results are conservative. Moreover, the fluctuations in photochemical efficiency from start to finish in seedlings growing in wet scalps were apparently of no consequence to growth as of yet.

In the diverse conditions of the field, the chlorophyll fluorescence method used for diagnosing physiological trauma in Scots pine seedlings came across as being more sensitive than in the greenhouse experiments. However, this “greater sensitivity” could very well be due to the combination of stressful forces stirring up unrest in seedlings in scalps. In any case, while dark-adapted  $F_v/F_m$  of needles has been shown to be less sensitive to early or moderate stages of drought stress (as in Studies II and III), it is not yet clear—especially in field conditions—just how long solely poor aeration due to waterlogged peat soil must continue before infringing upon photochemical efficiency in Scots pine. Potentially,  $F_v/F_m$  could be more sensitive to the effects of mechanical injury like bud and shoot damage than waterlogged soil, or vice versa.

Several similarities in the stress response of Scots pine seedlings pervaded both the greenhouse and field results. Generally,  $F_v/F_m$  was higher in current-year than previous-year Scots pine needles, and increased the gap in  $F_v/F_m$  between the two. In addition, without exception old needles responded first to both drought and waterlogging stress, thus providing the first indication of internal upset. Therefore, new needles were prioritized as old needles bore the initial burden. Finally, terminal leader shoot growth was clearly negatively affected by stress occurring during shoot elongation. This conflicts somewhat with the idea that shoot length of Scots pine is predetermined by the previous season’s bud formation and the prevailing conditions at that time (Clements 1970, van den Berg and Lanner 1971, Kozłowski et al. 1973, Lanner 1976, Junttila and Heide 1981, Salminen and Jalkanen 2005). According to that principle, the length of the new shoot largely depends on the number of stem (growth) units established during apical bud formation (Junttila and Heide 1981, Junttila 1986, James et al. 1994, Salminen and Jalkanen 2005). In this case, apical buds were formed the previous season in plush nursery conditions. Consequently, here stress inhibited fulfillment of the predetermined shoot growth pattern without delay in the summer of 2009, but additionally would have “delayed” consequences for the next growing season on account of suboptimal growing conditions during bud formation (e.g., Dobbertin et al. 2010).

### 4.3. Impact of soil preparation on greenhouse gas fluxes

#### 4.3.1. $CO_2$

On the upside, soil preparation succeeding clearcutting in a drained nutrient-poor peatland did not markedly affect the overall annual flux of  $CO_2$  from the soil to the atmosphere in the short term (Study IV). In fact, the magnitude of heterotrophic soil respiration here coincides with the results of Ojanen et al. (2010) from drained, forested peatlands of equivalent fertility. On the downside, however, neither low nor high intensity preparation of peat soil accelerated decomposition in



planting spots, which through increased nutrient mineralization would have been beneficial from the regeneration aspect (Study I). This finding conspicuously contrasts with previous inferences regarding the benefits of mounding to tree seedlings (Kaunisto and Päivänen 1985, Sutton 1993, Paavilainen and Päivänen 1995, Londo and Mroz 2001).

Previously, Bulmer et al. (1998) and Prescott et al. (2000) suggested that the impact of soil preparation measures on organic matter decomposition will depend on the total area disturbed in addition to the severity of the disturbance. Considering the enormity of the disturbance caused by the mounding treatment (Study IV, Table 1), its impact on heterotrophic respiration of peat soil alone ( $SR_p$ ) was altogether trifling (Study IV, Fig. 10a). However, the fact that unprepared microsites remaining in prepared plots released more  $CO_2$  not only compared to mounds, pits, and scalps, but also the unprepared microsites in the control treatment, seemingly indicates that the conditions for peat decomposition, e.g., aeration, soil temperature, substrate quality, were actually improved (or disturbed) by the presence of nearby prepared patches. At the same time, it may signify the destructive impact of heavy machinery (first during clearcutting and then soil preparation) driving over the remaining vegetation. Such trampling would inevitably break roots and other plant organs, and thus possibly boosted the deposition of organic substances, i.e., litter and root exudates, into the rhizosphere before collars were even installed or measurements began.

Contrary to many earlier studies employing the closed chamber technique on forestry-drained peatlands (e.g., Mäkiranta et al. 2008, Ojanen et al. 2010), WTL rather than soil temperature was more influential concerning the observed rates of  $SR_p$ . This was caused by exceptionally high WTLs (relative to soil surface of microsites), especially in the Northend block. Instantaneous  $SR_p$  in unprepared microsites, not prepared ones, exhibited the greatest dependency on soil temperature. Similar to the observation made by Mäkiranta et al. (2010) after clearcutting, the temperature sensitivity of  $SR_p$  clearly suffered here as the moisture level rose. Along the same line, in their litterbag experiment Laiho et al. (2004) also identified a negative or lacking temperature effect on the decomposition of needle and root litter in drained peatlands, which they attributed to drought in the former case and oxygen deficiency in the latter case.

The inherent above and below peat surface variation in WTL in scalps and pits, for instance, made parameterization of efflux models virtually impossible. While runoff flowed into scalps and pits during heavy rainfall and temporarily elevated  $SR_p$  (Study IV, Fig. 6), this contamination effect wore off and the water in the microsite became stagnant. A shortage of oxygen likely deterred microbial respiration since the  $SR_p$  rate dropped radically during these subsequent rain-free periods. In addition, the installed aluminum collars retained standing water atop poorly permeating peat surfaces consequently influencing gas dynamics. Also previously, trenching has been implicated in increasing soil moisture within compared to outside the collared microsite (Subke et al. 2006, Mäkiranta et al. 2008).

Notably, the mean WTL was higher in the unprepared microsites within the mounded plots than those in the control plots for both blocks (Study IV, Table 2). Upon closer examination, the mounding method applied at Joenvarsisuo incapacitated transpiring vegetation over a wide area (Study IV, Table 1) and could actually have contributed further to watering up of mounded plots, consequently reducing soil aeration and thus  $SR_p$ . Such an effect on  $SR_p$  is evident namely in mounds and pits as Study IV, Fig. 3a indicates. Many studies have concluded that water loss by evapotranspiration (via wetland vegetation) is greater than from open water (Nichols and Brown 1980, Verry 1997). The importance of vegetation and its interaction with the WTL, reflected in evapotranspiration rates, has been widely recognized in peatland hydrology (Laine 1984, Verry 1988). Since clearcutting removes all trees and thus the majority of the living, transpiring plant biomass which in effect raises the WTL (Heikurainen and Päivänen 1970, Dubé et al. 1995, Roy et al. 1997), it seems warranted to speculate that ground and field vegetation removal to the pro-

portion of that achieved at Joenvarsisuo by mounding could extend this trend. As a result, soil processes like microbial respiration are inevitably impacted.

The albeit puzzling finding regarding the non-effect of creating peat mounds on  $SR_p$ , synchronized with the results of Mojeremane (2009) from afforested sites on peaty gley soils. The potential reasons for this result are not however unfathomable. First of all, mounds primarily consisted of old, rather decomposed peat, the quality of which is far from ideal from the viewpoint of microbes. As pointed out by Hogg et al. (1992), some deeper peats are resistant to decay no matter if the soil becomes better aerated and warmer. Byrne and Farrell (2005) likewise identified such a situation in blanket peatland sites where despite significantly different WTLs,  $CO_2$  emission rates remained the same. Prescott et al. (2000) also touched on this topic in their overview of humus, indicating that environmental factors and substrate quality on nutrient-poor and more acidic sites may ultimately limit peat decomposition despite drainage. Furthermore, several studies have noted that the accumulation of certain substances in the deeper soil layers (e.g., lignins and phenolic or humic substances), which are unfavorable for microbial activity and thus decomposition, could be responsible for the decay resistance (e.g., Ivarson 1977, Dickinson 1983, Freeman et al. 2001). As Laiho et al. (2004) also pointed out, decomposers responsible for early and advanced organic matter decay may have different moisture and temperature optima. Consequently, a shift in the strength of the moisture versus temperature response may occur as the chemical quality of the decaying material undergoes change.

As an indicator of substrate quality, soil C:N ratio is often used to describe decomposition of organic matter (e.g., Enríquez et al. 1993). Higher C:N ratios are generally understood to limit decomposition due to a shortage in available nitrogen and an abundance of recalcitrant material. In the comparison between planting spots (mounds, scalps, control microsites) in Study I, in fact, the smallest C:N ratio and greatest N concentration were linked to the fastest rate of decomposition in the Northend (control microsites), while similar C:N ratios and N concentrations led to equal rates of decomposition in the Southend (control microsites and mounds). Surprisingly, on the whole mounding succeeded in reducing the N concentration in the surface peat and increasing the C:N ratio (Study I), which contradicts previously presented inferences on the subject (Kaunisto and Päivänen 1985, Sutton 1993). Nitrogen concentrations generally increase towards deeper peat layers and with the degree of decomposition on oligo-ombrotrophic sites (e.g., Kaunisto 1982, Laiho et al. 1999), and this should have brought higher concentrations on the top of mounds. On the other hand, Laiho et al. (1999) also showed the difference in N concentration between the topmost and deeper peat layers to decline as the time since initial drainage increased on oligo-ombrotrophic sites. In their study, the oldest drainage age class was between 41–55 years, whereas the Joenvarsisuo site was considerably older having been drained nearly 80 years ago. Thus, the declining trend they observed may have been even more apparent here, shown as the N enrichment of the topmost, now upturned, peat. Depending on the effectiveness of drainage in different parts of the peatland, peat subsidence and hence the thickness of the N enriched layer may also vary (Laiho et al. 1999).

In mounds, the most readily decomposable organic material is located at the bottom. Especially in the Northend block, the WTL commonly rose to a distance of as little as 5 cm from this layer of fresh carbon. Though aerobic fungi and bacteria are most ubiquitous in addition to being the most influential and effective microbial decomposers of OM in the upper layers of the peat profile where the input of new carbon is greatest (e.g., Blodau et al. 2003, 2004, Peltoniemi 2010, Straková 2010), burying their food into a low oxygen environment may have disrupted the decomposition process. Mojeremane (2009) previously reported that a lack of oxygen confined decomposition at the bottom of mounds. Regarding the diffusion of  $CO_2$  through soil into the atmosphere, Smith et al. (2003) emphasized the role of soil aeration and water content. In this

case, it would appear that  $\text{CO}_2$  was more easily diffused into the atmosphere from the “active layer” in an unprepared microsite than from the poorly aerated mound bottom through the denser, recalcitrant peat summit. Furthermore, the final step of the mounding technique applied at the Joenvarsisuo site also involved compaction of the peat mound. The effect of this maneuver on peat aeration and thus decomposition is difficult to deduce without equivalent measurements from uncompacted mounds. No intentional mixing of the excavated peat occurred, and this in itself could also have restricted decomposition in mounds, for mixing has been shown to stimulate microbial activity via increased soil aeration and temperature (e.g., Armentano and Menges 1986, Davidson et al. 1998, Mojeremane 2009).

#### 4.3.2. $\text{CH}_4$

$\text{CH}_4$  production, oxidation, and emission are largely controlled by the depth of the water table (e.g., Crill et al. 1988, Roulet et al. 1993, Martikainen et al. 1995). The contrasting results between blocks (Northend vs. Southend) for  $\text{CH}_4$  fluxes (Study IV, Figs. 3b and 10b) are telltale of the consequences of poor versus sufficient drainage. Moreover, the potential for increased  $\text{CH}_4$  production and emission can be heightened by soil preparation in sites with an already high WTL. Here, the clear difference in annual  $\text{CH}_4$  flux between the mounding and control treatments in the Northend (Study IV, Fig. 10b) implies that the requirements for  $\text{CH}_4$  production and emission were best fulfilled after mounding. This may also be construed as an intensification of watering up.

Watering up would also cause mire vegetation, such as cottongrass, to flourish as observed here particularly in the Northend mounding treatment plot. As a deep-rooting species, cottongrass not only transports  $\text{CH}_4$  through the root-shoot pathway hence preventing oxidation inside the plant, but also releases organic material necessary for  $\text{CH}_4$  production into the anaerobic peat layers (Schütz et al. 1991, Thomas et al. 1996, Tuittila et al. 2000).

Where drainage is sufficient (e.g., here in the control and mounding treatment plots in the Southend of Joenvarsisuo), the effect of soil preparation on  $\text{CH}_4$  emissions is of little concern at least in nutrient-poor clearcut peatland forests. In Study IV, the magnitude of annual  $\text{CH}_4$  emission even from the Northend mounding treatment was in any case small, but if applied in richer peatland sites characterized by a high WTL, the story may be wholly different. To reduce  $\text{CH}_4$  efflux and the potential for watering up in sensitive sites, a method of mounding which avoids the creation of open pits and smothering of intact vegetated surfaces is recommendable based on the observations of Study IV. Instead, inverted mounding would be more appropriate.

Though  $\text{CH}_4$  emission has typically been observed to decrease as the water table deepens in peatlands (Roulet et al. 1993, Nykänen et al. 1998) and even in bare peat surfaces (Tuittila et al. 2000), high  $\text{CH}_4$  emission associated with a declining WTL during the growing season has also been witnessed on natural peatlands with a fluctuating WTL as well as those under restoration (Shannon and White 1994, Komulainen et al. 1998). This latter-mentioned phenomenon was observed here in scalps where emission peaks occurred namely when the WTL dropped as illustrated in Study IV, Fig. 7. Since gas diffuses more rapidly via air-filled rather than water-filled pores, it is likely that the sogginess of scalps slowed down gas movement, and when the WTL eventually dropped,  $\text{CH}_4$  was finally able to diffuse with greater ease leading to  $\text{CH}_4$  bursts. Similarly, on a rewetted forestry-drained ombrotrophic bog, Komulainen et al. (1998) attributed such  $\text{CH}_4$  peaks to the reduction of pressure as the WTL fell which then enabled the release of  $\text{CH}_4$  stored below the water table.

Despite the sogginess of both scalped plots,  $\text{CH}_4$  emission rates were startlingly low (Study IV, Fig. 10b). As described above,  $\text{CH}_4$  diffusion in scalps was likely hindered by surplus water, but

in addition scalps lacked vegetation, which would have consequences for both plant-facilitated  $\text{CH}_4$  transport as well as substrate supply to methanogens for  $\text{CH}_4$  production (Tuittila et al. 2000). Unprepared microsites in the scalping treatment, however, had vegetation intact and were not waterlogged. They released  $\text{CO}_2$  at over three times the rate of scalps but  $\text{CH}_4$  emission was nevertheless equally low, which seemingly attests to decent soil aeration.

#### 4.3.3. $\text{N}_2\text{O}$

Low nitrification activity and lack of nitrate, which in effect limit  $\text{N}_2\text{O}$  production, have been previously observed in ombrotrophic mires (e.g., Martikainen et al. 1993). Though the magnitude of  $\text{N}_2\text{O}$  emission was also low in Study IV, soil preparation did apparently enhance the availability of ammonium and nitrate for nitrification and denitrification relative to the control since  $\text{N}_2\text{O}$  levels were higher namely in the mounding and scalping treatments (Study IV, Figs. 3c and 10c). Since the unprepared microsites of the control treatment were fully vegetated unlike mounds and scalps, any nitrate produced would likely have been more efficiently assimilated by plants in them. Thus, a nitrate shortage due to plant uptake could have limited  $\text{N}_2\text{O}$  production in the control treatment. Moreover, in scalps and pits the potential for denitrification clearly existed due to the constant intercourse with the water table and resultant anoxic conditions. According to Askaer et al. (2010), soil moisture changes dynamically in peat soils and even small precipitation events can create anaerobic microforms, which promote the formation of  $\text{N}_2\text{O}$ .

In accounting for these flux differences, there is also the case of the unprepared microsites in the mounding and scalping treatments to consider. As with  $\text{CO}_2$  emission, they emitted clearly more  $\text{N}_2\text{O}$  than those in the control treatment, but this difference cannot be due to a lack of vegetation cover or contrasting species composition. Possibly, the application of soil preparation disturbs the residual patchwork of vegetation, e.g., by damaging roots, and hence reduces their capacity to use free nitrate. At the same time, the heavy machinery inevitably incapacitates at least some of the remaining vegetation when in operation, whether it be through direct dismemberment of plant organs or soil compaction. As conveyed earlier in Section 4.3.1., dying plants replenish the soil with new organic matter, which would thus intensify decomposition leading to increased nitrate formation. The fact that the rate of decomposition in these unprepared microsites within the mounding and scalping treatments (Study IV, Fig. 3a) clearly exceeded the rate of those in the control treatment supports this idea.

Along the same line, the control treatment plots underwent only a single major disruption (clearcutting), while the mounding and scalping treatment plots experienced two (clearcutting and soil preparation). Additionally, the resultant watering up (and suspected reduction in evapotranspiration from soil) particularly after mounding presumably heightened denitrification and the  $\text{N}_2\text{O}$  flux from the soil. For instance, Mäkiranta et al. (2012) noted that increased soil moisture under logging residues likely increased the potential for denitrification and  $\text{N}_2\text{O}$  emission. Watering up after clearcutting and soil preparation would appear to drive the same end.

Although input of N through logging slash cannot be overruled here, the extent of it should have been more or less equal in all treatment plots since they were all clearcut. In addition, the amount of logging residues was limited by the low volume of the harvested pine stand. Unfortunately, C:N was not determined from the substrate of  $\text{N}_2\text{O}$  microsites, thus the possible role of C:N in regards to  $\text{N}_2\text{O}$  fluxes cannot be defined here. In any event, having materialized in a nutrient-poor peatland site, the occurrence and intensity of this phenomenon—accelerated  $\text{N}_2\text{O}$  emission after soil preparation—on richer sites are yet to be determined.

## 5. CONCLUSIONS

This dissertation investigated the impacts of soil preparation after clearcutting Scots pine forest on thick-peated soil from silvicultural and climatic standpoints. As an intensive method of soil preparation, mounding most effectively secured seedling survival, growth, and vitality—regeneration success—through improved soil aeration of the planting spot. However, other presumed benefits of mounding to seedlings such as warmer soil temperatures and faster organic matter decomposition (and thus enhanced nutrient release to soil) were not confirmed here. Since mounds were mainly composed of old recalcitrant peat with a high carbon-to-nitrogen ratio in addition to being poorly aerated at the bottom (due to a high WTL) where the best quality OM was actually located, no positive effect on decomposition resulted. Furthermore, the mounding procedure likely disturbed the microbial community by, for example, burying their food supply in the unfavorable conditions at the mound bottom.

After three growing seasons, regeneration in scalps was unsuccessful due to waterlogged soil. Hence, scalping should only be applied on well-drained sites, preferably with a mean WTL 40–50 cm below the soil surface, and definitely not before ensuring an adequate degree of drainage in the regeneration site. When scalping it is also of utmost pertinence to avoid disrupting the exposed peat surface, i.e., only the humus layer should be scraped off without creating overly deep depressions. In hydrologically sensitive sites, leaving the soil unprepared would seem a wiser option than scalping. Here, planted Scots pine seedling growth in unprepared microsites matched that achieved in mounds.

Scots pine seedling tolerance to adverse soil water conditions—surplus versus shortage—in genuine peat soil *over one growing season* was remarkable in controlled conditions. Although mortality was limited for both drought and wet-stressed seedlings, all in all drought caused more immediate and severe changes in seedling morphology, physiology, and metabolism. Drought stress markedly reduced root and shoot growth, fractional colonization of ectomycorrhizal fungi, as well as root hydraulic conductance, but maintenance of rather high potential photochemical efficiency (dark-adapted  $F_v/F_m$ ) despite severe drought stress would seem to indicate a potential for seedling recovery if water availability in the peat substrate improved. Polyamine analysis revealed that new needles are preferred in protecting the different parts of the seedlings against drought stress. Contrarily, seedlings were for the most part unfazed by waterlogged soil over one growing season and thus wet stress was the lesser of two evils.

Apparently, waterlogging does not modify seedling growth immediately, but rather in the longer term. These findings suggest the existence of a “window for recovery” in wet-stressed Scots pine seedlings; should a wet growing season be followed by a relatively normal one, then the consequences for growth are likely minimal. However, as the regeneration survey at the Joenavarsisuo site indicated, high water level and copious rainfall in *back to back* growing seasons has a devastating effect on outplant survival and growth (in scalps).

Furthermore, it was also demonstrated how the experimental environment—a controlled versus field setting—influences seedling biology and tolerance to stress. In fact, in field conditions, the wetter the soil, the lower  $F_v/F_m$ . Although other causes of distress, primarily browsing damage, were indeed involved, poor soil aeration due to waterlogged soil contributed to notable declines in photochemical efficiency of previous-year needles in seedlings planted in scalps. Nevertheless, the differing moisture levels within *comparable* microsites—dry vs. wet scalps and ditch vs. inverted mounds—had little influence on seedling growth and condition although a physiological consequence (i.e.,  $F_v/F_m$ ) was evident within scalps. Thus, it would appear that the type of scalp



(*wet* or *dry* based on median WTL) or mounding technique used (*ditch* or *inverted*) is irrelevant at least when considering the well-being of outplanted seedlings after the first growing season. Moreover, the fluctuations in photochemical efficiency from start to finish in seedlings growing in wet scalps were apparently at no expense to growth.

In the response of Scots pine seedlings to stress, three general trends stood out. Firstly, photochemical efficiency ( $F_v/F_m$ ) was typically higher in current-year than previous-year Scots pine needles, and *stress increased the gap in  $F_v/F_m$  between the two*. Secondly, previous-year needles provided the first indication of physiological trauma as  $F_v/F_m$  declined and *current-year needles were, in effect, prioritized as old needles bore the initial burden*. Thirdly, terminal leader shoot growth was clearly negatively affected by stress occurring *during* shoot elongation, which conflicts with the idea that shoot length of Scots pine is predetermined by the previous season's bud formation and the prevailing conditions at that time (e.g., Lanner 1976). Hence, *stress inhibits fulfillment of the fixed shoot growth pattern in addition to undermining bud formation, the consequences of which carry over into the next growing season*.

According to this dissertation, the fear of soil preparation accelerating GHG emissions, particularly  $\text{CO}_2$ , from peat into the atmosphere appears unwarranted at least on nutrient-poor, boreal forestry-drained peatland sites. The overall climatic impact of soil preparation, in the forms of mounding and scalping, three years after application expressed in terms of  $\text{CO}_2$  equivalents (100-year GWP), was neutral. Nonetheless, soil water relations were pivotal in determining  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  flux rates from both prepared (mounds, scalps, and pits) and unprepared microsites. Notably, unprepared microsites, not prepared ones, within the mounding and scalping treatment plots, accounted for the greatest rates of  $\text{SR}_p$  (i.e., decomposition from organic matter). Thus, it appears that soil preparation stimulates decomposition namely in the residual patchwork of intact vegetation. This interesting, previously unreported side effect was also transparent with regards to  $\text{N}_2\text{O}$  emission. However, neither mounding (inclusive of mounds, pits, and residual unprepared microsites) nor scalping (inclusive of scalps and residual unprepared microsites) accelerated annual  $\text{SR}_p$  relative to the control treatment. Both soil preparation treatments, on the other hand, increased the annual flux of  $\text{N}_2\text{O}$  from peat soil compared to the control.

Annual fluxes of  $\text{CH}_4$  were dependent on the position of the water table. The mounding treatment apparently intensified watering up of the clearcut site in part due to the creation of deep open pits. The high water table also fueled the spread of cottongrass, a known  $\text{CH}_4$  transporter, and in effect, the mounding treatment produced the greatest annual  $\text{CH}_4$  emissions. All in all, GHG emission levels were low but synchronized with those from forestry-drained sites of equivalently low fertility (Ojanen et al. 2010). Thus, despite the unique GHG flux behavior associated with different types of *prepared* and *unprepared microsites*, the apparent differences cancelled each other out when considering their comprehensive effects at the *treatment level*. Moreover, though the soil preparation treatments were applied in blocks with conspicuously opposing hydrological conditions, in the end this was of negligible importance. Nevertheless, this dissertation suggests that there are previously unidentified risks involved with preparing soil in ditched but nonetheless wet peatlands. In doing so, we may inadvertently alter the dynamic processes governing GHG emissions.

The core findings of this research support mounding as the best alternative on nutrient-poor, drained peatland sites when the goal is to maximize the regeneration success of Scots pine after clearcutting with minimal impact on soil GHG emissions. This is especially true where the water table level remains high (approximately  $\leq 30$  cm below peatland surface) due to ineffective drainage and when summertime rainfall is abundant. During the course of this investigation, too much rather than too little water in peat soil was the supreme force to be reckoned with in field

conditions. However, should climate change increase the occurrence and intensity of drought periods in the boreal forest zone, this would likely alter not only the regeneration success of Scots pine outplants in peat mounds but also the role of environmental factors controlling soil GHG emissions from such sites as here.

In light of the phenomena described and validated by this work, many unresolved questions remain to be answered in the future. With regard to the impacts of soil preparation on GHG emission from peat soil, the next step will be to implement larger scale, long-term experiments on drained sites in forestry use representing a range of soil fertility classes and drainage effectiveness. Additionally, special attention should be paid to modeling  $SR_p$  in prepared, bare peat microsites (mounds, scalps, and pits), whose  $CO_2$  flux behavior—and the factors driving it—distinctly differ from undisturbed microsites which have typically been modeled in GHG studies concerning forestry-drained peatlands. Importantly, this implies recognition and detailed characterization of precipitation events and their interaction with the exposed peat substrate and prevailing WTL in determining  $SR_p$  rates. With respect to the regeneration and tolerance of Scots pine seedlings to water-associated stress on peat soils, it will be necessary to examine seedling vulnerability to *long-term* drought and waterlogging as well as recovery in both prepared and unprepared planting spots. This would help in distinguishing the “outer limits” of seedling stress tolerance “in the real world” for the benefit of practitioners involved in peatland forest regeneration. Finally, the number of studies dealing with the viability of different soil preparation methods (and no preparation) and consequences for regeneration success on forestry-drained peatlands are still limited. While it may not be the sexiest research topic in the worldwide rat race of the modern day, it is nonetheless of substantial importance in a country highly specialized not only in the utilization but also the rejuvenation of wood resources on drained peatlands.



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